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SEED MORPHOLOGY IN NORTH AMERICAN CAMPANULACEAE¹

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ABSTRACT

Campanulaceae (excluding Lobeliaceae) in North America comprise four genera and 35 species of annual, biennial, and perennial herbs. Generic and specific circumscriptions have been treated variously, and studies of seeds have been few and limited. In this study, seeds of all but one of the native North American species and of selected Eurasian putative relatives were examined with the light and scanning electron microscope. Characteristics of the seeds and their surface cells are described and compared. The seed-coat morphology was found to be relatively uniform, but there are recognizable generic patterns and a number of distinctive individual species. Seeds of *Campanula americana*, *C. divaricata*, and the other eastern species of *Campanula* are each distinctive and do not show the relative uniformity seen within *Githopsis*, *Triodanis*, *Heterocodon*, and the western species of *Campanula*. Seeds of the recently rediscovered *C. robinisiae* and of the wide-ranging *C. aparinoides* are highly distinctive and would appear to set each of these species apart within the genus. However in *Triodanis*, *T. texana* stands apart. Seeds of *Campanula reverchonii* resemble those of *Triodanis coloradoensis* more than those of other campanulas. Brief speculation on the adaptive significance of seed-coat sculpturing and ornamentation is given.

The Campanulaceae, in the strict sense (excluding Lobeliaceae), are a worldwide family of 35 to 40 genera and perhaps 800 species. Estimates of the number of species have ranged from 600 to 1,000 (Avetisian, 1967; Gadella, 1974; Kovanda, 1978). The species are largely perennial herbs, but some are annuals, biennials, or even small shrubs. The family is confined mainly to north and south temperate regions, being replaced in tropical and subtropical regions by the Lobeliaceae. Only *Wahlenbergia*, with possibly 100 species or more (Thulin, 1975; Carolin, pers. comm., 1981), is well developed in, and in fact restricted to, south temperate regions, especially

Australia and South Africa. *Campanula*, the northern counterpart, is the largest genus of the family, comprising some 300 species. It is confined to the north temperate zone, with its center of diversity in Eurasia. Only 23 species occur in North America (Shetler, 1963; Heckard, 1969; Morin, 1980). Three-fourths of these are narrow endemics. Nearly half (11 spp.) of the North American species occurs in the California Floristic Province, and, of these, seven species are endemic there.

The family Campanulaceae is of similar size and diversity in Europe and Soviet Eurasia. *Flora Europaea* (Tutin, editor, 1976) records 13 genera

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and 208 species, *Flora SSSR* (Fedorov, 1957), 19 genera and 223 species. Of these species, the genus *Campanula* accounts for 69% and 67%, respectively. Even allowing for narrower generic concepts, the Russian bellflower flora shows a slightly greater generic diversity. By contrast, the North American Campanulaceae comprise only four genera and 35 species, of which 23, or 65%, belong to *Campanula*. Six (26%) of the latter species are clearly annuals, nearly three times the average percentage of annuals for the genus as a whole. Four of these annual species are found only in California. *Campanula americana* L. has long been considered to be an annual under most circumstances in the wild, but the recent experimental studies of its ecological life cycle by the Baskins (1984) have shown that at least in north-central Kentucky the species behaves as either a winter annual or a biennial.

In the Southern Hemisphere, the family shows limited diversity and is poorly represented except in South Africa, where there are seven, mostly small genera. Two of these, *Cephalostigma* and *Lightfootia*, Thulin (1975) has submerged in *Wahlenbergia*. The latter, with 46 species recognized by Thulin, is the only genus showing substantial diversification in South Africa. It is the only genus of the family found in Australia, where it has radiated at least as much as in South Africa, and in New Zealand, where a few species occur. In South America, where the closely related Lobeliaceae achieve their greatest diversity, the Campanulaceae are represented by only a few species in three genera, including *Wahlenbergia*.

The first and still the only worldwide monograph of Campanulaceae is the one published in 1830 by DeCandolle. He recognized 21 genera and 234 species. Schonland's (1889) systematic conspectus of the family, although badly outdated, is still a standard reference. Generic classification has continued to perplex students of the family, and the question of generic limits continues to draw attention as new lines of evidence are introduced (Avetisian, 1948, 1967, 1973; Charadze, 1949, 1970, 1976; Heidenhain, 1953; Fedorov, 1957; Carolin, 1960, 1967; Contandriopoulos, 1964, 1967, 1970a, 1970b, 1972, 1976; Gadella 1964, 1966; Phitos, 1964, 1965; Damboldt, 1965, 1970, 1975, 1976; Podlech, 1965; Kovanda, 1970a, 1970b, 1977; Dunbar, 1973, 1975a, 1975b; Thulin, 1975; Dunbar & Wallentinus, 1976).

Four genera of Campanulaceae are indigenous

to North America: *Campanula* (23 spp.), *Triodanis* (7 spp.), *Githopsis* (4 spp.), and *Heterocodon* (1 sp.). Three of the *Campanula* species have sometimes been placed in other genera. Small (1903) erected the genus *Campanulastrum* for *Campanula americana* (see also Shetler & Matthews, 1967) and the genus *Rotantha* (1933) for *Campanula floridana* S. Wats. ex A. Gray and *C. robinsiae* Small. McVaugh (1945a) placed *C. prenanthoides* Durand in the Eurasian genus *Asyneuma*. Added to the native species are about a dozen exotic species, introduced as ornamentals, that have escaped from cultivation and in some cases (e.g., *Campanula rapunculoides* L.) have become widely naturalized. At least eight species of *Campanula* are well established, as are the following other introduced taxa: *Jasione montana* L., *Legousia speculum-veneris* (L.) Chaix, *Platycodon grandiflorus* (Jacq.) A. DC.,⁴ and *Wahlenbergia* cf. *marginata* (Thunberg) DC.

Studies of the seeds of Campanulaceae have been few and limited (Corner, 1976). Seed characters have been little used in the systematics of the group, and a comprehensive study of surface morphology has never been made in this family as a whole. The advent of the scanning electron microscope (SEM) has rejuvenated the whole field of seed morphology (Brisson & Peterson, 1977), however. Among the spate of recent SEM studies are Geslot's (1980) survey of 17 European species of *Campanula* and the two studies dealing with campanulaceous genera by Thulin (1974, 1975), notably his survey (1975) of the seed coats of the species of *Wahlenbergia* in South Africa and Madagascar. Geslot concentrated particularly on *Campanula* subsection *Heterophylla*, examining 11 species of this group. Another important recent contribution is Carolin's (1980) SEM study of seed surfaces in *Goodenia* and related genera of the sister family, Goodeniaceae. Brief reports of our own study also have appeared in print (Morin & Shetler, 1981; Shetler & Morin, 1981).

In our study, we examined the seeds of 38 species of Campanulaceae—32 of the 35 indigenous species and six other species. Seeds could

⁴ The generic name *Platycodon*, compounded from the Greek, is to be treated as a masculine noun (Stafleu, 1978, Art. 74; Stearn, 1966), not a neuter noun, as proposed originally by Alphonse DeCandolle (1830). Accordingly, the correct name for the balloon flower is *P. grandiflorus*, not *P. grandiflorum*, as published by DeCandolle and almost universally followed by others since then.

not be obtained for three of the native species—*Campanula chamissonis* Fedorov (*C. dasyantha* auct.), *C. shetleri* L. Heckard, and *C. wilkinsiana* Greene. The other species examined were: *Asyneuma canescens* (Waldst. & Ket.) Griseb. & Schenck, *A. limonifolia* (L.) Janchen, *Legousia hybrida* (L.) Delarbre, *L. pentagonia* (L.) Druce, *L. speculum-veneris* (L.) Chaix, and *Triodanis falcata* (Ten.) McVaugh. Of the 38 species examined, only 36 are discussed here: *Asyneuma limonifolia* and *Legousia speculum-veneris* are not included.

Together, *Githopsis*, *Heterocodon*, and *Triodanis* comprise 12 species of indigenous small annuals. *Githopsis*, a genus that has perplexed taxonomists over the years, is found on the west coast of North America from Baja California Norte north to British Columbia. Species of the genus have narrow leaves and clavate capsules that dehisce at the apex by a perforation where the style breaks away. Ewan (1939) reviewed *Githopsis* and recognized seven species. Morin (1983), who revised the genus after studying breeding systems in the group, recognized just four species, including one cleistogamous (autogamous) species with rudimentary flowers, and several subspecies. In the monotypic *Heterocodon*, which also occurs on the west coast from California to British Columbia but extends east to Idaho, Montana, and Nevada, the short, broad capsule dehisces by irregular pores or fissures near the base. Both chasmogamous and cleistogamous flowers are produced regularly, as in *Triodanis*.

Triodanis comprises eight species, seven in North America and one in Eurasia (McVaugh, 1945b; Tutin, 1976). Traditionally they have been included in the genus *Specularia*, now *Legousia*. Tutin (1976), in *Flora Europaea*, retained *T. falcata* in *Legousia*. The genus is characterized by narrowly spiciform inflorescences, tiny cleistogamous early flowers in the lower axils that have vestigial corollas, chasmogamous upper flowers with rotate corollas, and slender, cylindrical or prismatic capsules that open by lateral pores. *Triodanis* can be distinguished from *Legousia* on the basis of the presence of cleistogamous flowers and the relative breadth of the capsules (McVaugh, 1945b, 1948). *Triodanis* species are plants largely of dry open habitats of the plains and canyons of the west and southwest, although *T. perfoliata* (L.) Niewl. and *T. biflora* (R. & P.) Greene (both of which extend into South America) are wide-ranging weeds of disturbed habi-

tats, often growing intermixed. In addition to the seven indigenous species, we also examined the seeds of the Mediterranean *T. falcata*. For comparison, we studied *Legousia hybrida* and *L. speculum-veneris*.

The genus *Campanula* is morphologically heterogeneous. It ranges across North America but is concentrated in the west. It is predominantly a genus of temperate montane, especially subalpine, habitats in North America as well as Eurasia. A few species inhabit truly alpine or arctic habitats. Shetler's (1963) annotated checklist is the only recent synopsis of North American species. He (1982) also has made extensive studies of the Nearctic harebells, the *C. rotundifolia* complex. The four California annual species were treated by Morin (1980), while the annual or biennial *C. americana* has been studied by Shetler (1958, 1962) and Baskin and Baskin (1984). No one has ever produced an infrageneric classification of the American campanulas, and one of the objects of the present study was to examine seed features for evidence of species clusters.

METHODS AND MATERIALS

Seeds for this study were taken from mature capsules of herbarium specimens on deposit in the herbarium of the University of California, Berkeley (UC), the New York Botanical Garden (NY), and the U.S. National Herbarium (US), Washington, D.C. (Table 1). Measurements were made with an ocular micrometer and stereoscopic microscope. Size of sample per collection, N, was 10 seeds whenever possible, but in some cases only a few seeds were available. Variation was assessed qualitatively by examining seeds from three different populations for each species when possible (Table 1). Seeds were examined under the scanning electron microscope, with as many seeds of a species being mounted on one stub as available or possible. The dried seeds were prepared for SEM study by first rehydrating them with aerosol and then dehydrating them in an alcohol series. From 100% ethanol, the seeds were placed directly into the chamber of a Denton DCP-1 Critical Point Drying Apparatus. After being critical-point dried, the seeds were mounted on SEM stubs with "Elmer's glue" (a water-soluble, animal-based glue) and sputter-coated with carbon and gold-palladium. Sectioned seed coats were obtained by both hand sectioning and spontaneous fracturing. They were examined and photographed in a Cambridge Stereoscan, either the Mark IIA or S410. In a

TABLE 1. List of vouchers of species studied. The "S" numbers are the seed sample numbers, which are used in the figure legends. Unless otherwise indicated, all vouchers are deposited at the U.S. National Herbarium (US).

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- Asyneuma canescens* (Waldst. & Kit.) Griseb. & Schenck
S072, Hungary (?), Transylvania, Olim, Richter, 12 August 1908
- Asyneuma limonifolium* (L.) Janchen
S071, Turkey, Taurus Mts., near Gulek Bogaz ("Gulek-Boghas") pass (= Cilician Gates), Balansa 627
- Campanula americana* L.
S013, Pennsylvania, Allegheny Co., Glenshaw, Jennings 307a
S014, North Carolina, Buncombe Co., Craggy Mt., Biltmore Herbarium 293b
S015, Canada, Ontario, Amherstburg, Macoun 54140
S016, Alabama, Blount Co., near Blountsville, Kral 37831
- Campanula angustiflora* Eastwood
S029, California, Lake Co., Spring Mt., Morin 249 (UC)
S055, California, Lake Co., Manning Flat, Bacigalupi & Sweeney 3346 (JEPS)
S056, California, Sonoma Co., Hood Mt., Baker 11756 (JEPS)
S057, California, Lake Co., Mirabel Mine, Eastwood & Howell 5530 (JEPS)
S058, California, Santa Cruz Co., Boulder Creek, Hesse 100a (JEPS)
S059, California, Santa Cruz Co., Boulder Creek, Hesse 100b (JEPS)
- Campanula aparinoides* Pursh
S060, Minnesota, Clearwater Co., Itasca State Park, Grant 2848
S061, New York, Crystal Lake, McCall, 15 August 1877
S062, Canada, Quebec, Ile Salaberry (Salaberry de Valleyfield, now Valleyfield), Rouleau 4256 (UC)
S063, Indiana, Lagrange Co., Adam Lake, Yuncker & Welch 10717
- Campanula aurita* Greene
S086, Alaska, Walker Lake, Shetler 4962
- Campanula californica* (Kell.) Heller
S017, California, Mendocino Co., Point Arena, Davy & Blasdale 6056
- Campanula divaricata* Michaux
S018, Virginia, Augusta Co., Elliott's Knob, Steele 68
S019, Kentucky, Whitley Co., Cumberland Falls, McFarland 49
S020, Virginia, Page Co., Stony Man Mt., Lehtonen & Morin, 17 October 1980
- Campanula exigua* Rattan
S064, California, Contra Costa Co., Mt. Diablo, Bowerman 330 (JEPS)
- Campanula floridana* S. Watson ex A. Gray
S021, Florida, Levy Co., near Cedar Key, Godfrey 56612
S022, Florida, Manatee Co., Manatee ("Manitee," now Bradenton), Garber, April 1876
- Campanula griffinii* Morin
S028, California, San Benito Co., Clear Creek, Griffin 4120 (UC)
S084, California, Napa Co., south of Pope Valley, Breedlove 5047 (JEPS)
S085, California, Lake Co., Mirabel Mine, Eastwood 5530 (JEPS)
- Campanula lasiocarpa* Cham.
S023, Alaska, Aleutian Is., Attu, Turner 4296
S024, Canada, Yukon Territory, Mt. Sheldon, Porsild & Breitung 11731
S025, Alaska, Cook Inlet, Iliamna Point, Gorman, 1 September 1902
- Campanula parryi* A. Gray
S026, Colorado, Clear Creek Co., Georgetown, Patterson 97
S027, Colorado, Archuleta Co., Pagosa Springs, Wooton 2873
- Campanula piperi* Howell
S083, Washington, Clallam Co., Hurricane Ridge, Shetler 4430
- Campanula prenanthoides* Durand
S007, California, Siskiyou Co., Humbug Mt., Butler 1815
S008, California, Humboldt Co., Willow Creek, Tracy 3286
S009, Oregon, Jackson, Siskiyou Mts., Heller 13486
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TABLE 1. Continued.

<i>Campanula reverchonii</i> A. Gray
S010, Texas, Burnet Co., Granite Mt., <i>Palmer 10266</i>
S011, Texas, Burnet Co., Marble Falls, <i>Biltmore Herbarium 14893</i>
S012, Texas <i>Nealley 149</i>
<i>Campanula robinsiae</i> Small
S090, Florida, Hernando Co., Chinsegut Hill, <i>Cooley, Wood & Wilson 6029 (NY)</i>
<i>Campanula rotundifolia</i> L.
S087, Alaska, Kodiak I., <i>Shetler & Stone 3622</i>
S088, Colorado, Park Co., near Lake George, <i>Shetler & Dick 3903</i>
S089, New York, Tompkins Co., Taughannock Gorge, <i>Vogelmann 603</i>
<i>Campanula scabrella</i> Engelm.
S030, California, Siskiyou Co., Mt. Eddy, <i>Eastwood 2010</i>
S031, California, Siskiyou Co., Scott Mts., <i>Engelmann, 30 August 1880 (GH)</i>
S032, Washington, Wenatchie Region, <i>Brandegge 937 (GH)</i>
S065, California, Siskiyou Co., Mt. Eddy, <i>Raven 10415 (JEPS)</i>
<i>Campanula scouleri</i> Hook. ex DC.
S005, Washington, Skamania Co., Mt. Prindle, <i>Suksdorf 11769</i>
S006, California, Humboldt Co., Rio Dell, <i>Moldenke & Moldenke 20338</i>
<i>Campanula sharsmithiae</i> Morin
S066, California, Stanislaus Co., Red Mt., <i>Sharsmith 3144 (UC)</i>
<i>Campanula uniflora</i> L.
S001, Canada, Baffin I., Frobisher Bay, <i>Collins 109</i>
S002, Canada, Quebec, Poste de Payne Bay, <i>Rousseau 1280</i>
S003, Canada, Hudson Bay, Belcher Is., <i>Abbe, Abbe & Marr 4030</i>
S004, Canada, White I., Frozen Straits, <i>Angel 37</i>
<i>Githopsis diffusa</i> A. Gray subsp. <i>diffusa</i>
S078, California, Santa Barbara Co., San Roque Canyon, <i>Pollard, 31 May 1952 (UC)</i>
<i>Githopsis diffusa</i> subsp. <i>candida</i> (Ewan) Morin
S079, California, San Diego Co., N of Santa Ysabel, <i>Munz 9806 (UC)</i>
<i>Githopsis diffusa</i> subsp. <i>filicaulis</i> (Ewan) Morin
S082, California, Riverside Co., Sage, <i>Morin 234 (UC)</i>
<i>Githopsis diffusa</i> subsp. <i>robusta</i> Morin
S077, California, Lake Co., Elk Mt., <i>Koch 960 (UC)</i>
<i>Githopsis pulchella</i> Vatke subsp. <i>pulchella</i>
S080, California, Amador Co., Drytown, <i>Greene, June 1889 (UC)</i>
<i>Githopsis pulchella</i> subsp. <i>serpentinicola</i> Morin
S081, California, Tuolumne Co., Yosemite Junction, <i>Mason 11108 (UC)</i>
<i>Githopsis specularioides</i> Nutt.
S075, California, Humboldt Co., Alder Point, <i>Tracy 1906 (UC)</i>
S076, California, Shasta Co., near Redding, <i>Hoover 2279 (UC)</i>
<i>Githopsis tenella</i> Morin
S074, California, Kern Co., Greenhorn Mt., <i>Morin 241 (UC)</i>
<i>Heterocodon rariflorum</i> Nutt.
S052, California, Marin Co., Mt. Tamalpais, <i>Herman 17388</i>
S053, California, Trinity Co., Stuart Fork of Trinity R., <i>Alexander & Kellogg 5546</i>
S054, Oregon, Washington Co., Hillsboro, <i>Howell 1036</i> ; A = chasmogamous flowers, B = cleistogamous flowers
<i>Legousia hybrida</i> (L.) Delarbre
S067, England, Devonshire ("Devon"), ex herb. Hore, 13 July 1826 (" <i>Prismatocarpus hybridus</i> ")
<i>Legousia pentagonia</i> (L.) Druce
S070, Greece, Aegean Sea, Rhodes (Rodhos) I. ("Isola di Rodi"), <i>Vaccari 513</i>
<i>Legousia speculum-veneris</i> (L.) Chaix
S069, Italy, Bay of Naples, Capri I., <i>Guadagno, May 1905 ("<i>Specularia hirta</i>")</i>

TABLE 1. Continued.

<i>Triodanis biflora</i> (R. & P.) Greene	
S046,	Kansas, Woodson Co., near Yates Center, <i>Lathrop</i> 545
S047,	Missouri, Baxter, <i>Bush</i> 15601; A = chasmogamous flowers, B = cleistogamous flowers
S048,	California, Humboldt Co., Klamath R., <i>Chandler</i> 1415
<i>Triodanis coloradoensis</i> (Buckley) McVaugh	
S033,	Texas, Gillespie Co., Crab Apple, <i>Jermy</i> 468; cleistogamous flowers sampled (" <i>Specularia lindheimeri</i> ")
S034,	Texas, Kerr Co., Kerrville, <i>Heller</i> 1731; A = chasmogamous flowers, B = cleistogamous flowers (" <i>Specularia lindheimeri</i> ")
S035,	Texas, Bexar Co., <i>Jermy</i> 29 (" <i>Specularia lindheimeri</i> ")
<i>Triodanis falcata</i> (Ten.) McVaugh	
S068,	Cyprus, Palaeokhora, <i>Sintenis & Rigo</i> , 24 September 1880
<i>Triodanis holzingeri</i> McVaugh	
S036,	Colorado, Las Animas Co., near Troy, <i>Rogers</i> 4646
S037,	Arizona, Pima Co., near Sells, <i>Lehto, Brown, Nash & Pinkava</i> 10738
S038,	Oklahoma, Kiowa Co., near Snyder, <i>Waterfall</i> 13103
<i>Triodanis lamprosperma</i> McVaugh	
S039,	Arkansas, Garland Co., Hot Springs National Park, <i>Adams</i> , 6 May 1960
<i>Triodanis leptocarpa</i> (Nutt.) Nieuwl.	
S040,	Oklahoma, Comanche Co., Mt. Scott, <i>Waterfall</i> 13075
S041,	Kansas, Woodson Co., <i>Lathrop</i> 448
S042,	Texas, Tarrant Co., Fort Worth (" <i>Polytechnic</i> "), <i>Ruth</i> 140; A = chasmogamous flowers, B = cleistogamous flowers
<i>Triodanis perfoliata</i> (L.) Nieuwl.	
S043,	Kentucky, Lewis, Big Sulphur Creek, <i>Braun</i> 4021
S044,	Tennessee, Sevier Co., near Gatlinburg, <i>Miller</i> 2300
S045,	Maryland, Prince Georges Co., College Park, <i>McVaugh</i> 1483
<i>Triodanis texana</i> McVaugh	
S049,	Texas, Denton Co., Denton, <i>Whitehouse</i> 15839; A = chasmogamous flowers, B = cleistogamous flowers
S050,	Texas, Dallas Co., Dallas, <i>Bush</i> 680
S051,	Texas, San Patricio Co., near Aransas Pass, <i>Whitehouse</i> 18204

few cases, where shriveling was minimal, the dried seeds were mounted, coated, and examined directly from the herbarium specimens.

Seed coats also were examined and photographed under the light microscope. The seeds were soaked briefly in "aerosol OT," and the coats were teased off, stained with 0.1% Tolidine Blue O, and mounted on a glass slide in Hoyer's solution. Camera lucida drawings of these peels were made for many of the species, and a selection of them is included here.

RESULTS

GENERAL DESCRIPTION

The seeds of North American Campanulaceae are generally quite smooth, except in some cases under relatively high magnification (500× or more). Ornamentation of the seed coat is minimal, and only a few species stand out as having noteworthy features. Based on features of seed

surfaces, the genera or species-group form relatively homogenous assemblages. In our study, size, shape, and surface pattern tended to be consistent within a given species.

The seeds of all but a few species are elliptical, oblong, or more or less round in outline (Table 2). The cells of the seed coat (testa) usually are fibriform (narrowly fusiform) with thickened, lignified radial walls (Table 3). The surface pattern of the seeds under low magnification is rugose (shallow furrows), reticulate, or striate in most species, depending on the degree of tangential wall collapse (Table 2). When the outer tangential walls have collapsed only slightly, the pattern might be described by Murley's (1951) term *favulariate*, used in her light-microscope studies of crucifer seeds. When these walls have collapsed completely, the seed coat is conspicuously striate or even ribbed (Fig. 26). Tubercles or ridges (enhanced striation) may result from differential thickening of the radial walls (Figs. 35, 38–40,

113, 117). The degree of verrucosity may vary from seed to seed even within the same capsule.

The inner and perhaps the outer tangential walls often are differentially thickened in rings, spirals, or more irregular patterns (Figs. 100, 120, 121). The radial walls also may have thickenings on their inner faces (Figs. 101, 110, 112). The outer or top edges of the radial walls may be smooth or thickened more or less regularly in a pattern of ornamentation that gives the surface of the seed coat a beaded or pebbled appearance (Figs. 35, 38, 39, 113, 117). On the surface, the radial walls may appear to be beaded on the long axis and ridged or upturned at the ends, which gives the surface a wavy or pebbled appearance. In some species there are superficial, noncellular tuberculae or excrescences.

In cross-section, seed shape ranges from terete or oval (Figs. 88–92, 95) to lenticular (Figs. 93, 94, 96, 99) or even triangular (Fig. 97) or quadrangular (Fig. 98; Table 2). Rounded seeds may be flattened asymmetrically toward one rib (Fig. 91). Most of the seeds are truncated at least somewhat at the hilum end and are more or less rounded at the other end. Even in the fusiform seeds, which taper more or less to a point at each end, the hilum end tends to be squared off. In some species, the hilum end is an organized, well-marked, symmetrical region (e.g., *Campanula americana*, Fig. 94), while in many other species this end is little more than an asymmetrical slit or pinched-off zone (Figs. 88–93).

The radial walls of testa cells may be thin and the lumen large and open (Figs. 102, 103), or thick and the lumen narrow and slit-like (Figs. 109, 111) or hour-glass-shaped in cross-section, as when the radial walls are rod-like (Figs. 106, 107, 112). In some cases (not depicted), the lumen appears to be widest in the middle and the radial walls somewhat hour-glass-shaped. Some species have pitted radial walls (Figs. 102–104, 120c), and at least one species, *C. floridana* (Fig. 105), has large, irregularly shaped foramina in the walls. Seed coats with cells that have thin radial walls and large lumina tend to have cells that are almost isodiametric in surface view and are deeper than long or wide (Figs. 102, 103, 120c). The area where the cells meet appears either as a trough or a ridge in some species, but in other species it can be observed only with difficulty if at all (cf. e.g., Figs. 14, 66, 108). The surface of the seed coat may have a relatively thick layer of non-cellular material or virtually none (cf. Figs. 44, 100–112). A distinct cuticle is

detectable in some species, as in *Triodanis texana* (Fig. 116).

The seed-coat cells of North American Campanulaceae can be divided into the three basic types described below. Cell type is indicated in Table 3 for every species studied.

Type 1. Cells elongate, fusiform or fibriform, with relatively thick radial walls and narrow, often indistinct lumen. The cells form a continuous weave without clearly squared, abutting end-walls and often without clear indication of where one cell ends and another begins (e.g., *Campanula griffinii*, Figs. 4, 120a).

Type 2. Cells trapezoidal or irregularly hexagonal with thick to moderately thick radial walls and narrow to relatively wide lumen. The cells form a distinct reticulum with obvious cell outlines and cell ends, even when the outer tangential walls have not collapsed. When the tangential walls collapse, the surface appears ribbed (e.g., *C. divaricata*, Figs. 34, 120b).

Type 3. Cells more or less isodiametric in face view, hexagonal or lobed, with large deep lumen and relatively thin radial walls having pits or foramina. The cells form a jigsaw-puzzle or quilted pattern (e.g., *C. aparinoides*, Figs. 31, 102, 120c).

CAMPANULA

The mature seeds range in length from 0.4 mm to 1.6 mm and in width from 0.2 mm to 0.9 mm, with the length/width ratio ranging from 1.0 to 3.3 (Table 2). The color ranges from buff to rich chestnut brown. The surface pattern is more or less reticulate (often appearing striate), the degree depending on the thickness of the radial walls, relative dimensions of the cells, and the extent of the tangential-wall collapse. The wider the cells, thinner the radial walls, and more collapsed the outer tangential walls, the more reticulate the surface pattern. The individual cells are the units of the reticulum. The narrower the cells, thicker the radial walls, and the more intact the outer tangential walls, the less reticulate and more striate or rugose the seed coat appears.

The Cordilleran campanulas, *C. scabrella* (Figs. 9, 10), *C. parryi* (Figs. 11, 12), *C. piperi* (Figs. 13, 14), and *C. aurita* (Figs. 15, 16), form a relatively homogeneous group based on seed characteristics. The widest-ranging of these, *C. parryi*, has the smallest seeds—0.5–0.6 mm long—distinguishing it from the larger-seeded (0.7–1.0 mm) *C. scabrella*, with which it sometimes is confused (Table 2). Closely similar are *C. uni-*

TABLE 2. Comparison of seed shape, size, surface, and presence and placement of wings of seeds of North American Campanulaceae and possible relatives.

Taxon	Shape		Approx. Length ¹		Surface	Wings ²
	Longitudinal	Cross-section	L/W (mm)			
<i>Asyneuma</i>						
<i>canescens</i>	long-ovate	ovate	1.6	2.2	shallow furrows)
<i>Campanula</i>						
<i>americana</i>	oblong	lenticular	1.3–1.6	1.5–1.7	pebbled	()
<i>angustiflora</i>	ovate	broadly ovate	0.7	2	faintly striate)
<i>aparinoides</i>	oblong	terete to triangular	0.7	1.3–2.3	shallowly colliculate	—
<i>aurita</i>	oblong	narrowly ovate	1.2	2	interrupted striate	()
<i>californica</i>	elliptical to ob- ovate	broadly ovate	0.9	1.7	interrupted striate	—
<i>divaricata</i>	oblong	terete	0.7	2	reticulate)
<i>exigua</i>	oblong	ovate	0.7	2	faintly striate)
<i>floridana</i>	broadly elliptical to quadrangu- lar	terete ovate	0.6	1.5	rugose)
<i>griffinii</i>	oblong	ovate	0.6–1.1	2.2	faintly striate)
<i>lasiocarpa</i>	fusiform to ovate	terete	0.7	2	striate	—
<i>parryi</i>	elliptical	terete	0.6	1.8	striate	∨
<i>piperi</i>	narrowly ellipti- cal	terete	0.7	2	striate	∧ ∨
<i>prenanthoides</i>	oblong	ovate-flattened	0.9	2.2	striate)
<i>reverchonii</i>	broadly elliptical- roundish	lenticular	0.9	1.3	striate	—
<i>robinsiae</i>	roundish	triangular	0.4	1	margins tubercu- late	—
<i>rotundifolia</i>	oblong	terete to ovate	0.8	2	striate)
<i>scabrella</i>	oblong	ovate	0.7–1.0	1.5–3.3	striate)
<i>scouleri</i>	oblong	ovate	1.0	2	striate-reticulate)
<i>sharsmithiae</i>	oblong	terete	0.8	2.6	smooth	—
<i>uniflora</i>	oblong	terete	1.0	2	striate)
<i>Githopsis</i>						
<i>diffusa</i>	fusiform	terete	0.6–0.8	3.0–3.8	striate)
<i>pulchella</i>	fusiform	terete	0.7–1.0	2.4	striate)
<i>specularioides</i>	fusiform	terete	0.8	2.6	striate)
<i>tenella</i>	fusiform	terete	0.7	1.8	flattened reticu- lum)
<i>Heterocodon</i>						
<i>rariflorum</i>	elliptical	terete	0.5	1.7–2.1	smooth	∧
<i>Legousia</i>						
<i>hybrida</i>	elliptical	terete	1.4	1.6	shallow furrows	—
<i>pentagonia</i>	elliptical	narrowly elliptical	1.5	1.6	shallow furrows	—
<i>Triodanis</i>						
<i>biflora</i>	broadly elliptical	lenticular	0.5	1.3	shallow furrows	()
<i>coloradoensis</i>	broadly elliptical	lenticular	0.8	1.4	shallow furrows	()
<i>falcata</i>	broadly elliptical	lenticular	0.8	1.4	shallow furrows	()
<i>holzingeri</i>	broadly elliptical	lenticular	0.5	1.5	scattered tubercles	()
<i>lamprosperma</i>	broadly elliptical to roundish	lenticular	0.9	1.2	shallow furrows	()

TABLE 2. Continued.

Taxon	Shape		Approx. Length ¹		Surface	Wings ²
	Longitudinal	Cross-section	L/W (mm)			
<i>leptocarpa</i>	broadly elliptical to ovate	lenticular	0.8	1.6	shallow furrows	()
<i>perfoliata</i>	broadly elliptical to roundish	lenticular	0.5	1.3	smooth or tuber- culate	()
<i>texana</i>	broadly elliptical	quadrangular	0.4	1.4		()

¹ See text for ranges. Approximate range given here only for exceptionally variable species.

²) = peripheral ridge on one side only; () = ridge essentially on entire periphery; ^ = ridge on hilum end; v = ridge on end opposite hilum.

flora (Figs. 17, 18), *C. rotundifolia* (Figs. 19, 20), and *C. lasiocarpa* (Figs. 21, 22). These seven compose what might be regarded as the most common or typical campanula seed type in North America. The cellular pattern is Type 1 with gradation to Type 2.

The California annuals, *Campanula angustiflora*, *C. exigua*, *C. griffinii*, and *C. sharsmithiae* (Figs. 1–8, 93), have seeds that are extremely smooth, almost featureless, except under high magnification, and even at 500× the surface may be flat and smooth, as *C. sharsmithiae* (Fig. 8). The latter species, only recently discovered (Morin, 1980), is a narrow serpentine endemic of the Mt. Hamilton endemic area of California. Its cucumber-shaped seeds tend to be larger, smoother, and more nearly terete than the seeds of the other three annual species. The four species have the Type 1 cellular pattern.

Campanula prenanthoides (Figs. 23, 24) and *C. scouleri* (Figs. 25–27), also west coast species, share a similar seed-coat morphology with a Type 2, or Type 1 grading to Type 2, pattern, and they stand somewhat by themselves. The seeds of *C. scouleri* are large, about 1 mm long and 0.5 mm wide. The surface pattern is reticulate and ribbed when the outer tangential walls are collapsed (Fig. 26), but quite smooth when they have not collapsed (Fig. 27). The *C. prenanthoides* seed is distinctive in cross-section, being round on one side and compressed to a margin or flange on the other side (Fig. 91). The seeds of *Asyneuma canescens* (Figs. 28, 29) are similar to those of *C. prenanthoides* and *C. scouleri* in shape and outline. In addition, all three species have thick-walled, fibriform cells.

The three marsh species of North America, *C. aparinoides*, *C. floridana*, and *C. californica*, have distinctive seeds. The seeds of *C. californica* are

generally similar to those of *C. prenanthoides* and *C. scouleri*. *Campanula californica* (Figs. 32, 33) also has large seeds (0.9 mm long) with a shape similar to these species, but these are less conspicuously biconvex and have more typically a Type 1 surface pattern. The surface cells are quite deep (Fig. 109), however, possibly resulting in enhanced bouyancy.

The seed coat of *C. aparinoides* (Figs. 30, 31, 120c) is unlike any other in the genus. The cells are Type 3, essentially isodiametric in surface view, resembling tiny “oyster crackers” that fit together in a quilted pattern. The individual cells (Figs. 102, 103) have a large deep lumen and thin radial walls that have small pits visible under high magnification (2,000×). In recent studies of the *C. aparinoides*-*C. uliginosa* complex, Cochran (1981; pers. comm.) has found seed differences and other taxonomic characters that, in her opinion, justify treating the two as distinct subspecies of *C. aparinoides*, instead of lumping them as a single taxon, as is now customary.

The seeds of *C. floridana* (Figs. 36, 37) are small (0.6 mm long) with a rugose surface pattern. The cells of the seed coat are trapezoidal or roughly hexagonal with a large lumen and can be classed as Type 2 (Fig. 121e). The seeds are more or less terete in cross-section (Fig. 89) and have radial walls that are thin and have large, irregular openings that impart a “Swiss cheese” appearance (Fig. 105).

In seed-coat pattern, *C. divaricata* (Figs. 34, 35, 120b), the Appalachian bellflower, shows no clear affinity to any other species, although it approaches the pattern in *C. floridana*. The seed coat is reticulate with trapezoidal or hexagonal cells that perhaps best exemplify Type 2. The radial walls are moderately thick to thin and the lumen is large. The most distinctive feature is

TABLE 3. Comparison of surface seed-coat cells.

Taxon	Type	Shape	Lumen	Wall Thickness
<i>Asyneuma</i>	2	fibriform 80 × 10 μm	narrow	thick
<i>Campanula</i>				
<i>americana</i>	1	fibriform 72 × 11 μm	narrow	thick
<i>angustiflora</i>	1	oblong 43 × 10 μm	medium	variable
<i>aparinoides</i>	3	isodiametric 30 × 19 μm	large	thin
<i>aurita</i>	1-2	oblong	narrow	thick
<i>californica</i>	1	oblong 52 × 8.6 μm	medium	medium
<i>divaricata</i>	2	broad-fibriform 71 × 18 μm	large	thin
<i>exigua</i>	1	broad-fibriform 42 × 4.5 μm	narrow	thick
<i>floridana</i>	2-3	isodiametric 62 × 29 μm	large	thin
<i>griffini</i>	1	fibriform 66 × 10 μm	narrow	thick
<i>lasiocarpa</i>	1-2	fibriform 94 × 10 μm	narrow	thick
<i>parryi</i>	1	broad-fibriform 50 × 9 μm	medium	thick
<i>piperi</i>	1	broad-fibriform 60 × 7 μm	narrow	thick
<i>prenanthoides</i>	2	fibriform 60 × 7 μm	medium	thick
<i>reverchonii</i>	1	fibriform 54 × 7 μm	narrow	medium
<i>robinsiae</i>	3	isodiametric	cell structure not visible unknown in peels	
<i>rotundifolia</i>	1-2	fibriform 70 × 10 μm	medium	thick
<i>scabrella</i>	1-2	fibriform 56 × 14 μm	medium	medium
<i>scouleri</i>	1-2	fibriform 72 × 7 μm	narrow	thick
<i>sharsmithiae</i>	1	irregular 52 × 11 μm	medium	thick
<i>uniflora</i>	1-2	fibriform 59 × 11 μm	narrow	thick
<i>Githopsis</i>				
<i>diffusa</i>	1-2	long-fibriform 109 × 6.9 μm	medium	thin
<i>pulchella</i>	1-2	fibriform 79 × 10 μm	broad	medium
<i>specularioides</i>	1	fibriform 89 × 8 μm	medium	medium
<i>tenella</i>	2	short-fibriform 49 × 9 μm	broad	medium
<i>Heterocodon</i>				
<i>rariflorum</i>	1	fibriform 62 × 8.4 μm	narrow	thick

TABLE 3. Continued.

Taxon	Type	Shape	Lumen	Wall Thickness
<i>Legousia</i>				
<i>hybrida</i>	1	fibriform 74 × 9.2 μm	medium	thick
<i>Triodanis</i>				
<i>biflora</i>	1	fibriform 96 × 6.4 μm	narrow	thick
<i>coloradoensis</i>	1	fibriform 51 × 8.6 μm	wide	medium
<i>falcata</i>	2	fibriform 55 × 9.2 μm	narrow	thick
<i>holzingeri</i>	1	fibriform 60 × 10 μm	narrow	thick
<i>lamprosperma</i>	1	fibriform 75 × 9 μm	narrow	medium
<i>leptocarpa</i>	1	fibriform 150 × 9.4 μm	narrow	thick
<i>perfoliata</i>	1	fibriform 71 × 8.85 μm	narrow	thick
<i>texana</i>	2–3	short-fusiform 54 × 15 μm	narrow	medium

the regularly beaded outer edge of the radial walls (Figs. 35, 113).

The three non-Californian annual, winter-annual, or biennial species—*C. americana*, *C. reverchonii*, and *C. robinsiae*—have their own distinct seed-coat patterns. The seeds of *Campanula americana* (Figs. 38–40, 94, 121a), a wide-ranging species of woodland borders in eastern North America, have fibriform cells with thick radial walls and a narrow lumen. The radial walls have dense spirals of apparent secondary thickenings. The end walls are thickened into ridges that give the surface a pebbled or verrucose ornamentation under a thick cuticle (Figs. 39, 40). The seed is lenticular in cross-section (Fig. 94) and has a definite winged margin or flange the whole way around. The hilum end is truncated, more organized than in other species, and outlined by the heavy, symmetrical flange as an oval area.

Campanula robinsiae (Figs. 41–44, 97, 118) has the smallest seeds recorded for the North American members of the genus (Table 2). The surface is very smooth, and the seed is trigonous in cross-section; the angles are distinctly ridged and each has irregularly placed, smoothly rounded tubercles along it (Fig. 97). The seed-coat cells (Fig. 118) are of Type 3, digitate or lobed, with the lobes interlocking with other cells like the pieces of a jigsaw puzzle.

Campanula reverchonii (Figs. 67, 68, 96), the

basin bellflower of the Edwards Plateau of Texas, has seeds that are quite similar to the seeds of *Triodanis* species. The seed is elliptical in outline and more or less lenticular in cross-section (Fig. 96). The seed coat has Type 1 cells with a rugose or striate appearance.

HETEROCODON

Heterocodon rariflorum (Figs. 84, 85) has small (0.5–0.6 mm long) elliptical seeds that are terete in cross-section. The surface is very finely striate, being composed of long, narrow cells of Type 1.

TRIODANIS

Triodanis seeds are lenticular to elliptical in outline and lenticular (biconvex) in cross-section (Fig. 99). Excepting *T. texana* (Figs. 54–56), the seed coats have Type 1 cells, and the surfaces appear rugose, striate, or smooth. *Triodanis perfoliata* (Figs. 45–48, 104, 119), *T. holzingeri* (Figs. 49, 50, 99), *T. biflora* (Figs. 51–53, 112), and *T. texana* (Figs. 54–56, 98) have seeds that are 0.4–0.6 mm long. *Triodanis coloradoensis* (Figs. 57, 58), and *T. lamprosperma* (Figs. 61, 62), as well as the European *T. falcata* (Figs. 59, 60), have seeds that are 0.8–0.9 mm long. The seeds of *T. leptocarpa* (Figs. 63–66), which are more elongate, are about 0.8 mm long. *Triodanis falcata*, the European species, apart from a somewhat

smoother seed coat, fits right into the seed pattern of this largely North American genus. The radial walls of *Triodanis* are thick and rodlike (Fig. 112) and may have pits (Fig. 104). The surface may be verrucose or pebbled (Fig. 119) from irregular thickenings. In *T. perfoliata*, some populations have smooth seeds, while other populations have seed coats that are finely tuberculate with the tubercles in lines (cf. Figs. 45–48). McVaugh (1945b) studied this variation quantitatively with the light microscope.

Triodanis texana (Figs. 54–56, 98, 121b) clearly stands alone, not just within the genus but in the North American Campanulaceae generally. In outline, the seed is similar in shape to other seeds of *Triodanis*, but in cross-section (Fig. 98) it is quadrangular rather than lenticular. The cell type is intermediate between 2 and 3, although many cells are almost isodiametric, if irregularly so. The outer cell surfaces, presumably the tangential walls, are strongly convex and covered by a definite cuticle, which can be seen peeling away intact in Figure 116. The cells form a braided surface pattern like the surface of a cord or rope with its interwoven strands.

Seeds of cleistogamous and chasmogamous flowers were examined in *T. leptocarpa* (Figs. 63–66) and *T. texana*, but no consistent differences were observed in seed-coat morphology between seeds of the chasmogamous and cleistogamous flowers.

GITHOPSIS

The mature seeds of *Githopsis* (Figs. 69–81, 110, 115) range in length from 0.6 to 1.0 mm and in width from 0.2 to 0.4 mm, with the length/width ratio ranging from 1.8 to 3.8 (Table 2). The seeds are fusiform, more or less tapering to both ends and are terete in cross-section (Fig. 92). The surface pattern is fibriform-rugose to fibriform-reticulate in *G. pulchella* (Figs. 76–79, 115). The pattern appears striate in low magnification owing to the longitudinal ridges of the radial walls and the troughs of the lumina (Fig. 115). The cells are Type 1, grading to Type 2 particularly in *G. pulchella* (Table 3). *Githopsis tenella* (Figs. 74, 75) has the most fibriform pattern with the smoothest surface, owing to the very narrow lumina. The subspecies of *G. diffusa* (Figs. 69–73) are all similar in their surface patterns, as are the subspecies of *G. pulchella* (Figs. 76–79). The radial walls are thick and rod-like—ropy in surface view. In general, they are wider

than the almost slit-like lumina, although the width of the lumen is variable in *G. diffusa* and relatively large in *G. pulchella*.

The seeds of the four species of *Githopsis* and their subspecies, as recognized by Morin (1983), are distinguishable primarily on the basis of size. *Githopsis tenella* seeds are the most distinctive of the four species because of the density and small size of the seed-coat cells.

DISCUSSION

Seed-coat morphology in the North American Campanulaceae is relatively uniform, but there are recognizable generic patterns and a number of distinctive patterns in individual species. *Githopsis* seeds, although clearly similar to seeds of the majority of *Campanula* species, stand together with their fusiform shape and similar surface patterns of cells that have thick, rounded radial walls that look inflated, almost sausage-like. Individual cells of the testa look like miniature inflatable rafts (Fig. 115).

The more or less lenticular seed with Type 1 cells and a fibriform surface pattern is consistent within *Triodanis*, although the seeds of *T. leptocarpa* (Figs. 63, 65) are more elongate and oval than in the other species. Mediterranean *Triodanis falcata* (Figs. 59, 60), which in *Flora Europaea* (Tutin, 1976) is treated as a species of *Legousia*, fits in well with the larger-seeded American *Triodanis* species, although in cross-section the seeds are more rounded than typical *Triodanis* seeds. The one species that does not conform, except in the oval outline, is *T. texana* (Figs. 54–56, 98, 116). Its quadrangular seeds with an undulating surface pattern have no counterpart either in the genus or the family in North America. The seed-coat cells are irregular, thick-walled sclereids (Fig. 121b).

Triodanis often is included in *Legousia* (*Specularia*). Indeed, the seeds of *Legousia pentagonia* (Figs. 86, 87) and *L. speculum-veneris* (not shown) are similar in shape (outline and cross-section), especially to the seeds of the large-seeded *Triodanis* species (Figs. 57–66). The large seeds of *Legousia hybrida*—largest of the seeds studied—are rounded rather than lenticular in cross-section, and the cells of the testa are quite different from those of *Triodanis* (cf. Figs. 111, 112). These two genera clearly cannot be separated easily on the basis of their seeds, although more study particularly of *Legousia* species is needed.

The seeds of *Campanula reverchonii* (Figs. 67,

96) show definite similarities to the seeds of *Triodanis*. *Campanula reverchonii* is endemic to the granitic Central Basin or Llano Area of the Edwards Plateau in central Texas (Correll & Johnston, 1970). All American species of *Triodanis* are found in Texas; two of the seven species, *T. coloradoensis* and *T. texana*, are endemic to Texas, the former to the Edwards Plateau. Further study is needed of the relationships of *Triodanis* to *C. reverchonii*, which is not unlike some *Triodanis* species in habit. The seed similarity may be the result of convergence through environmental selection.

The relationship of *Heterocodon* to other genera is uncertain. McVaugh transferred it to *Specularia* in 1941 but subsequently (1945b) divided this latter genus into *Triodanis* and *Specularia* (*Legousia*) and reinstated the genus *Heterocodon*. In this later paper McVaugh suggested that he was maintaining it as separate from *Campanula* primarily because of tradition. The seeds of *Heterocodon*, although at the other end of the size range, are more similar to those of *L. hybrida* than to those of the other two species of *Legousia* examined or to any of the other taxa studied by us. The similarity of *Heterocodon* seeds to *Legousia* seeds and the fact that *Heterocodon* and *Triodanis* regularly produce cleistogamous as well as chasmogamous flowers support the theory that *Heterocodon* belongs in the *Legousia-Triodanis* complex.

Within *Campanula*, some weak groupings can be made, but for the most part the individual exceptions are more notable than the common patterns. The California annuals form a small group of four species. However, the seed of *C. sharsmithiae* (Figs. 7, 8) has a more terete shape and a smoother surface than the other three, owing, apparently, to a thicker cuticular layer.

The position of *Campanula californica* in the genus is uncertain. On the basis of seed morphology, it does not belong with the other two species of marshes, swamps, and bogs—*C. aparinoides* and *C. floridana*. The seeds suggest that its affinities might be much closer to *C. scouleri* and perhaps *C. prenanthoides*. McVaugh (1945a) transferred *C. prenanthoides* to the Eurasian genus *Asyneuma* because of its deeply lobed corolla. The similarity between the seeds of *A. canescens*, *C. prenanthoides*, *C. scouleri*, and *C. californica* suggests to us that these species may be related to each other.

The western American perennial alpine species of *Campanula* have a more or less common seed

pattern, although with variation. Although they differ markedly in size, the seeds of *C. aurita* and *C. parryi* have a very similar surface pattern. These species have other morphological similarities and to some extent are ecological counterparts, with *C. aurita* occurring in the far northern Rocky Mountains (Brooks Range) and Yukon Tablelands and *C. parryi* occurring in the central and southern Rockies. The two Pacific Northwest species, *C. piperi* and *C. scabrella*, ecological counterparts in the Olympic Mountains and Cascade Mountains, respectively, have quite similar seed-coat patterns (Figs. 10, 14, 121c), which also are generally like the patterns of *C. aurita* and *C. parryi* (Figs. 12, 16, 121d). The Olympic Mountain bellflower, a local endemic, resembles a smaller version of *C. aurita*, but there also are morphological grounds for regarding it as closely related to the downy alpine bellflower (*C. scabrella*). The latter forms almost a morphological continuum with *C. parryi* in the Northwest, although seed size seems to be a reliable character for distinguishing between the species.

On the basis of the seeds, *Campanula uniflora* (Figs. 17, 18), which otherwise appears to have no close relatives, does not stand apart noticeably from the other perennial bellflowers of western North America.

In eastern North America, *Campanula* is heterogeneous with respect to seed-coat pattern. Each species stands more or less alone, although *C. divaricata* and *C. floridana* have the same type of epidermal cell pattern (Figs. 34–37, 120b, 121e). It is possible that these two species have been derived from a common ancestor, but this possibility has never been raised before. Both, but particularly *C. divaricata*, show some similarity in cell pattern to the more northern and wide-ranging *C. rotundifolia* (Figs. 19, 20, 108, 114). The distinctive beaded thickenings on the radial walls of *C. divaricata* (Figs. 35, 113) are encountered sometimes also in the western *C. parryi* (Fig. 117), but on general morphological grounds these two species appear to be unrelated.

Like the tall bellflower, *Campanula aparinoides* and *C. robinsiae* each stand apart from other taxa in the genus in North America. *Campanula aparinoides* does not appear to be closely related to *C. floridana* (Cochrane, pers. comm.), contrary to Shetler's (1963) earlier speculation on the basis of ecology and general morphology. The two have altogether different seed types (Figs. 30, 31, 36, 37, 89, 95, 120c, 121e), including

quite different epidermal cells, although in both species these cells are relatively thin-walled with large lumina and pitted or fenestrate radial walls (Figs. 102, 103, 105; see also Cochrane, 1981). Small (1926) initially considered *C. robinsiae* to be most closely related to *C. reverchonii* but later (1933) placed it, with *C. floridana*, in his genus *Rotantha* (Figs. 41–44, 67, 68, 96, 97). The seeds of these three species bear little resemblance to each other and certainly would not support this view.

Of all North American Campanulaceae, *C. robinsiae* has the most unusual and distinctive seeds. This raises new questions about the origin of this elusive species, thought possibly to be extinct until its recent rediscovery. It is a small annual of puzzling origin (Shetler, 1963), known only from its type locality at Chinsegut Hill, near Brooksville, Florida. It had not been seen in the wild since 1958 until the spring of 1983 when it was found in several vernal pools in the Chinsegut Hill area first by Steven Hill and subsequently by others, including the authors. Surprisingly, it was not mentioned in Ward's recent book (1979) on rare and endangered plants of Florida, presumably because it was thought to be extinct or of doubtful origin in the first place. As an annual, this species may go through cycles of abundance and sparsity, and, being so small and inconspicuous, it is easily overlooked even when fully developed. The unusual seed morphology deepens the mystery of this plant's affinities. If there is any justification for Small's genus *Rotantha*, it is the suite of characters that seems to isolate *C. robinsiae* from the other species. Further studies are being conducted by the authors in collaboration with Steven Hill.

The affinities of *C. americana*, the tall bellflower, also remain obscure. This highly distinctive species with dense spicate racemes of star-shaped, rotate flowers; tall, often much-branched stems; and annual or biennial habit was given its own genus, *Campanulastrum*, by Small in 1903. Although the basic floral morphology is campanuloid, it does not fit well into the typical concept of *Campanula*. Small's view appears to have increasing justification from palynological, cytological, and now seed evidence. The pollen grains are pantaporate, a condition unique to only a few species among many species with 3–4-porate grains in *Campanula* (Avetisyan, 1967). Chromosome number is $n = 29$, unique in the genus largely comprising species in the $n = 17$ -series (Gadella, 1964). Surely this is a derived

number, probably through hybridization. Seed-coat morphology also is unique. The upturned ends of the radial walls, which seem to be responsible largely for the pebbled surface, occur to a limited extent in *C. parryi* (Figs. 38–40, 117), but on other grounds these species do not appear to be related. The isolated position of *C. americana*, further underscored by Gadella's (1964) inability to cross it with other campanulas, led Shetler (Shetler & Mathews, 1967) some time ago to support its placement in the genus *Campanulastrum*. Gadella, puzzled by *C. americana*, suggested that a search should be made among species of *Asyneuma*, which also have deeply cut corollas, for the origins or relationships of *C. americana*. Interestingly, the seeds of *A. canescens* (Figs. 28, 29) and *C. americana* (Figs. 38–40, 121a) appear to have similar epidermal cell patterns beneath their cuticular layers.

The adaptive significance of seed-coat sculpturing and ornamentation has been little studied. The seeds of bellflowers (Campanulaceae) apparently are dispersed mainly by water, with gravity playing an important role among those species that grow on rock ledges and cliff faces (e.g., *C. rotundifolia*). The relatively smooth, rounded seeds seem to be streamlined to facilitate water dispersal, and the seeds have no obvious adaptations for animal or bird dispersal. They are small and insignificant as a source of food, and, with the exception of *Campanula robinsiae* (Figs. 41–44) and *Triodanis perfoliata* (Figs. 45–48), lack superficial processes or ornamentation that might enhance their chances of being carried by animals. In the case of these two species, the tubercles are so minute that it is doubtful they have any dispersal role with respect to animals. Possibly, ants play a role in the dispersal of some or all bellflowers, and one can hypothesize that such tiny processes as these might facilitate transporting the seeds when ants are the dispersal agents. *Triodanis perfoliata* is wide-ranging, and perhaps tubercles confer a selective advantage in dispersal at least in some environments. This species is variable with respect to seed-coat tubercles, and the ratio of tuberculate to non-tuberculate seeds varies not only from population to population but also from region to region (McVaugh, 1945b). What selective advantage, if any, is conferred by the tubercles or lack of them, is not known.

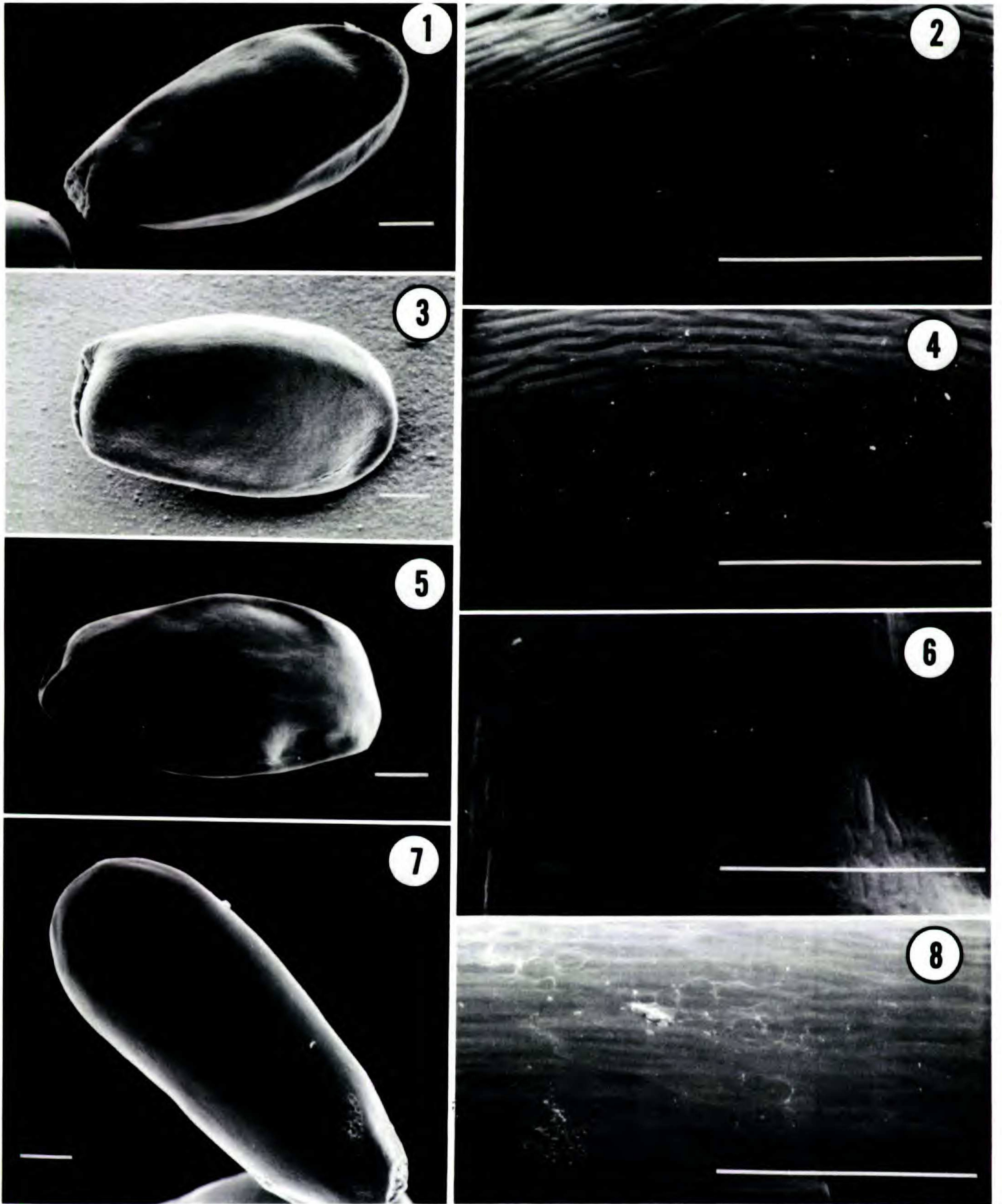
Two of the marsh/swamp species, *Campanula aparinoides* and *C. floridana*, have epidermal cells with relatively large lumina and thin walls that

have many pits or, in the case of *C. floridana*, large foramina (Figs. 102, 103, 105). Perhaps these cell characteristics give the seeds of these two species greater buoyancy in the hydric environment. At the same time, pits are not restricted to these species (cf. *Triodanis perfoliata*, Fig. 104).

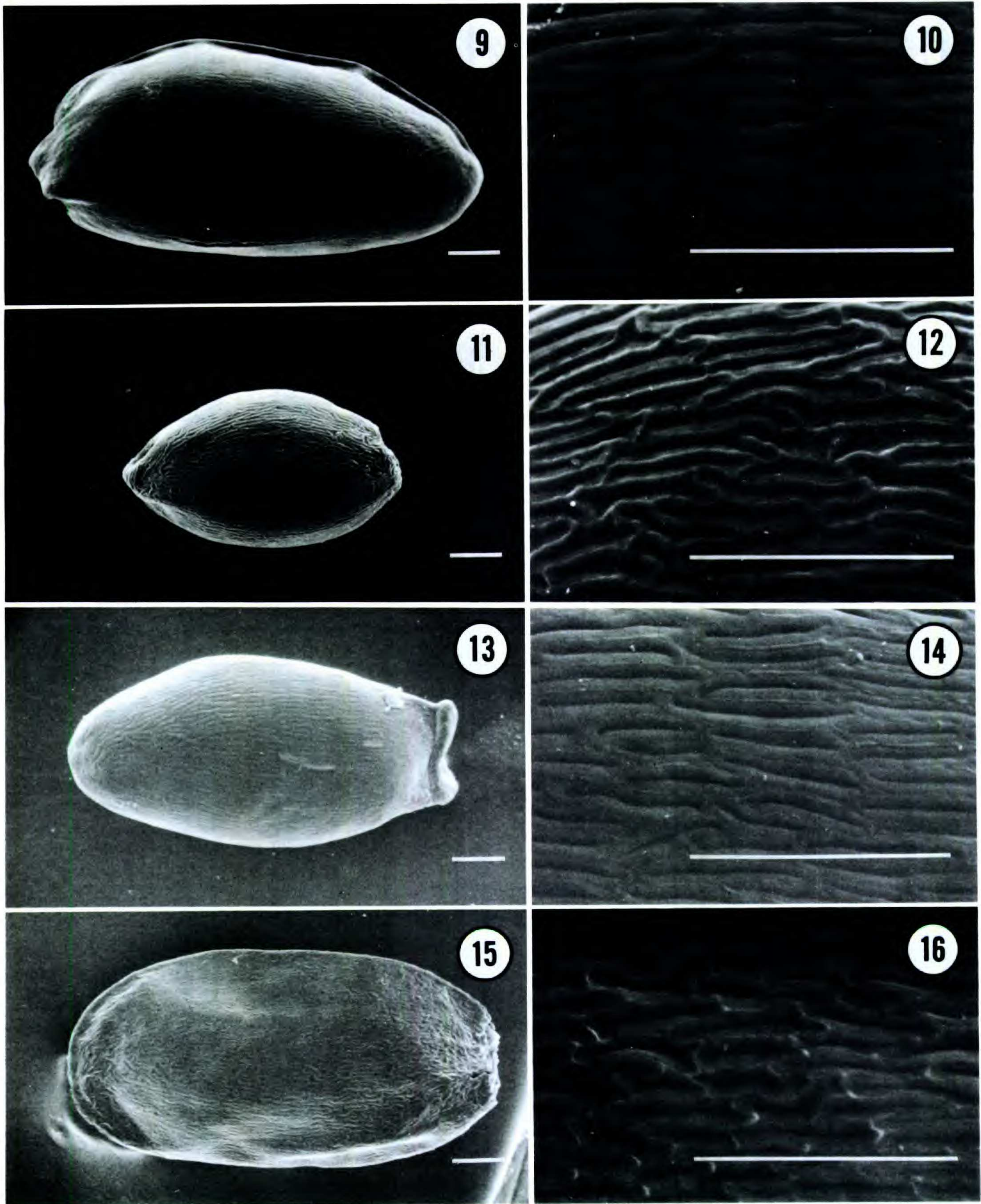
The seeds of the annual species have a "tight weave" of fibriform cells with thick radial walls that nearly fill the lumina and have a definite cuticle or layer of relatively smooth, non-cellular material on the outside of the testa. Perhaps such features have selective advantages in dry or disturbed habitats in preventing easy water-loss or water-logging by the seeds (Figs. 1-8, 38-40, 45-87).

Little is known about general trends of evolutionary specialization in seed-coat sculpturing, and the relatively few species of bellflowers in North America do not provide an adequate basis in themselves for reliable speculation about seed-coat phylogeny in the Campanulaceae. If there

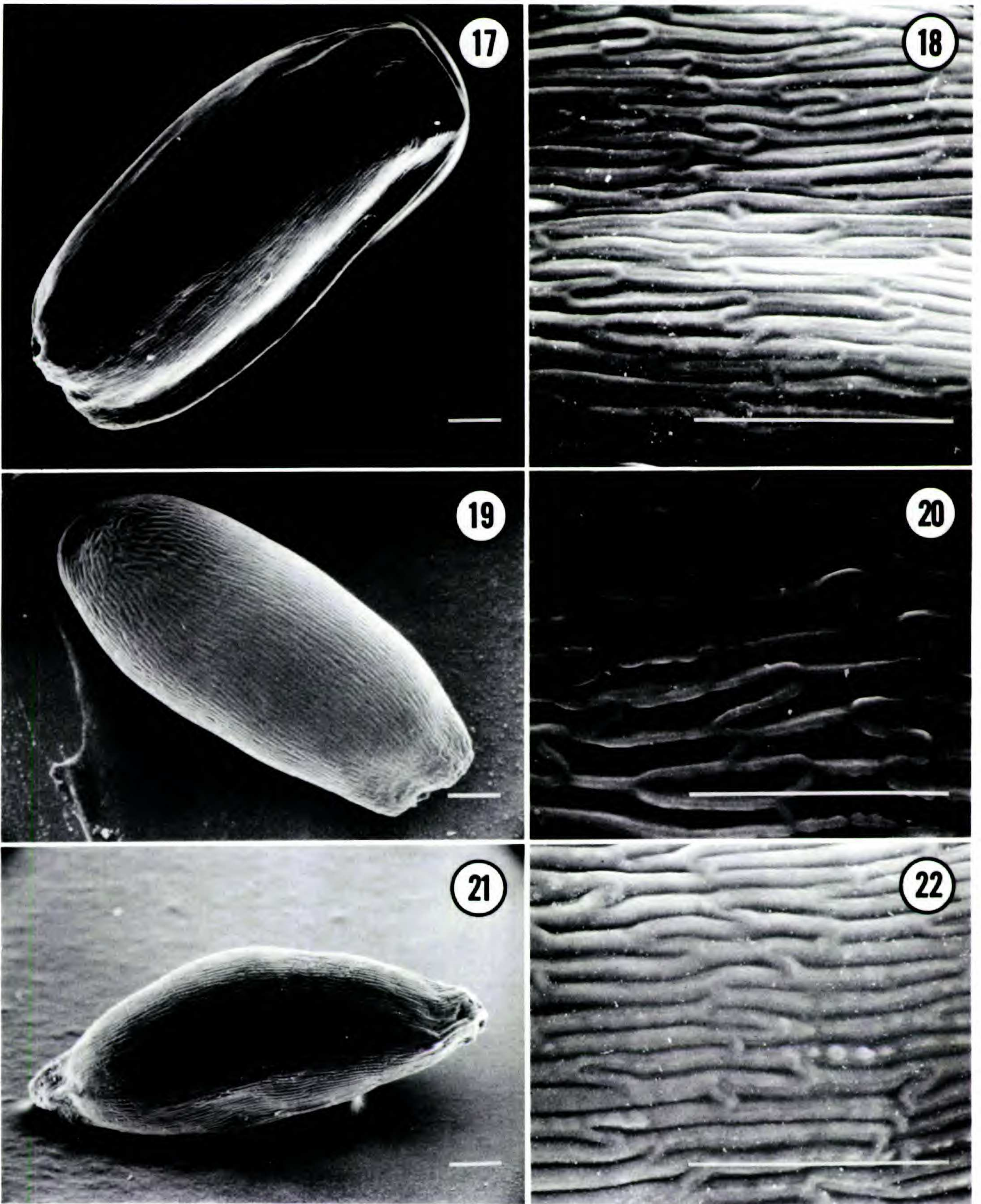
is a typical seed coat in North America, it would appear to be the type found among the western American perennial species. The annuals of the genus *Campanula* and of the family at large in North America, as well as the perennials in eastern North America (except *C. rotundifolia*) appear to represent several different tendencies in specialization of the seed coat. It is not clear whether these tendencies have evolved in North America in response to ecological or other selective factors, or represent tendencies to be found elsewhere in the family in Eurasia or perhaps even in the southern hemisphere in *Wahlenbergia*. Thulin's (1975) study of South African *Wahlenbergia* species shows some intriguing similarities in seed-coat sculpturing and seed shape. For instance, the pictured seed of *W. virgata* is very much like *Githopsis* seeds, and the seed of *W. subaphylla* resembles those of *Campanula prenanthoides*. Clearly, more study of the family worldwide is needed before the results presented here can be fully interpreted.



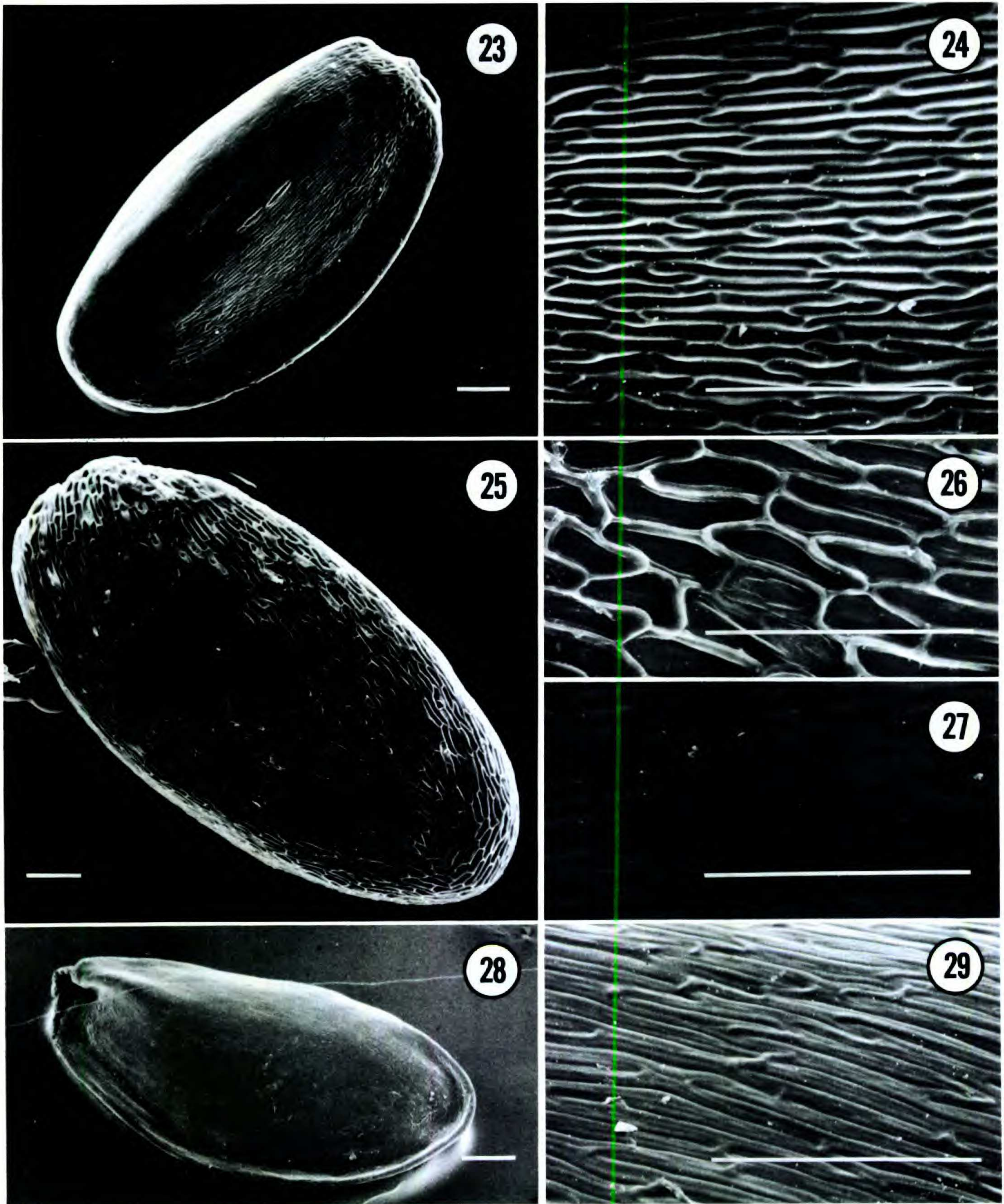
FIGURES 1-8 (bar = 100 μm). Seeds of annual *Campanula*.—Figures 1, 2. *Campanula angustiflora*.—1. Seed (S59).—2. Seed coat (S59).—Figures 3, 4. *C. griffinii*.—3. Seed (S85).—4. Seed coat (S28).—Figures 5, 6. *C. exigua*.—5. Seed (S64).—6. Seed coat (S64).—Figures 7, 8. *C. sharsmithiae*.—7. Seed (S66).—8. Seed coat (S66).



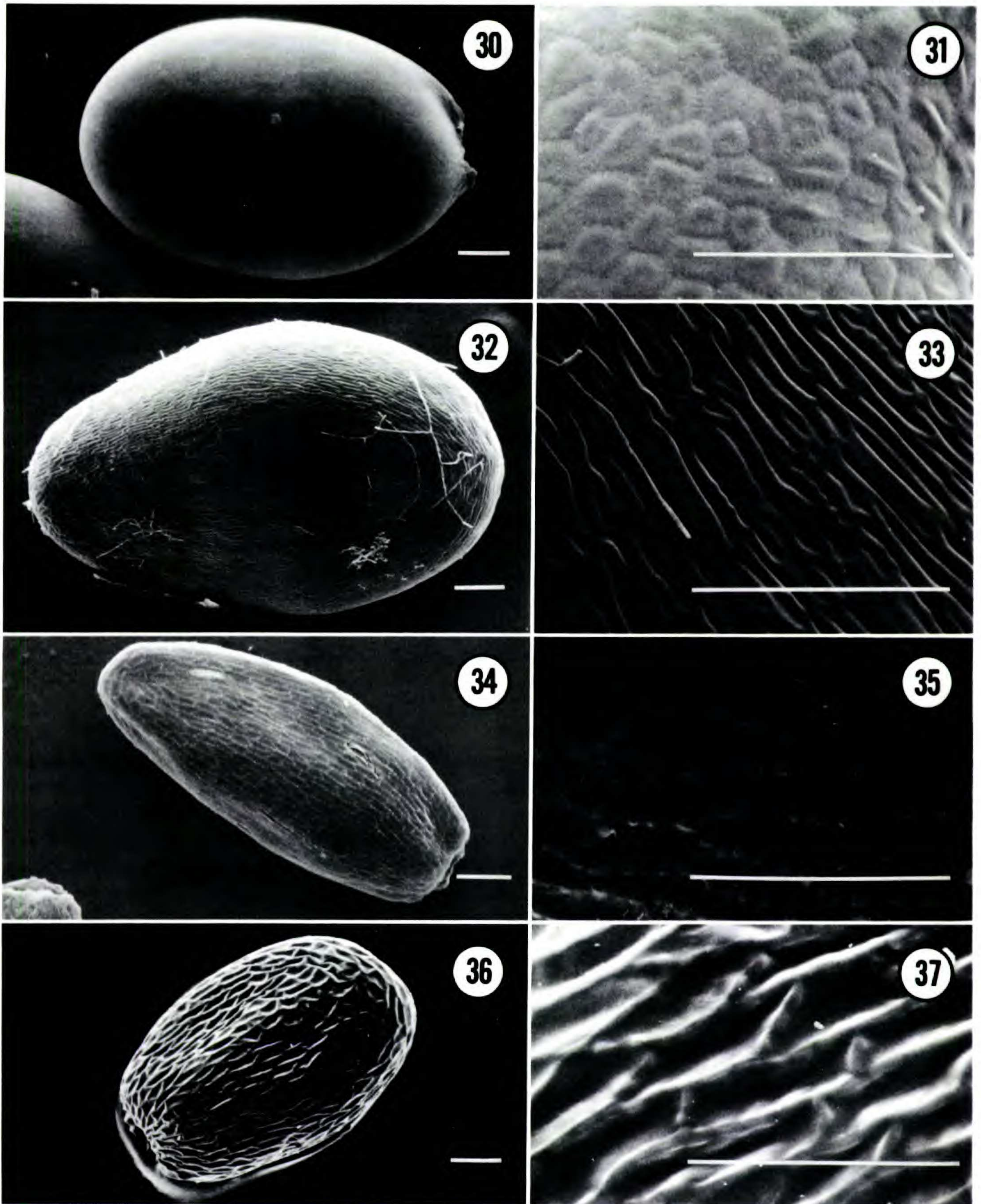
FIGURES 9-16 (bar = 100 μm). Seeds of perennial *Campanula*.—Figures 9, 10. *Campanula scabrella*.—9. Seed (S65).—10. Seed coat (S65).—Figures 11, 12. *C. parryi*.—11. Seed (S27).—12. Seed coat (S27).—Figures 13, 14. *C. piperi*.—13. Seed (S83).—14. Seed coat (S83).—Figures 15, 16. *C. aurita*.—15. Seed (S86).—16. Seed coat (S86).



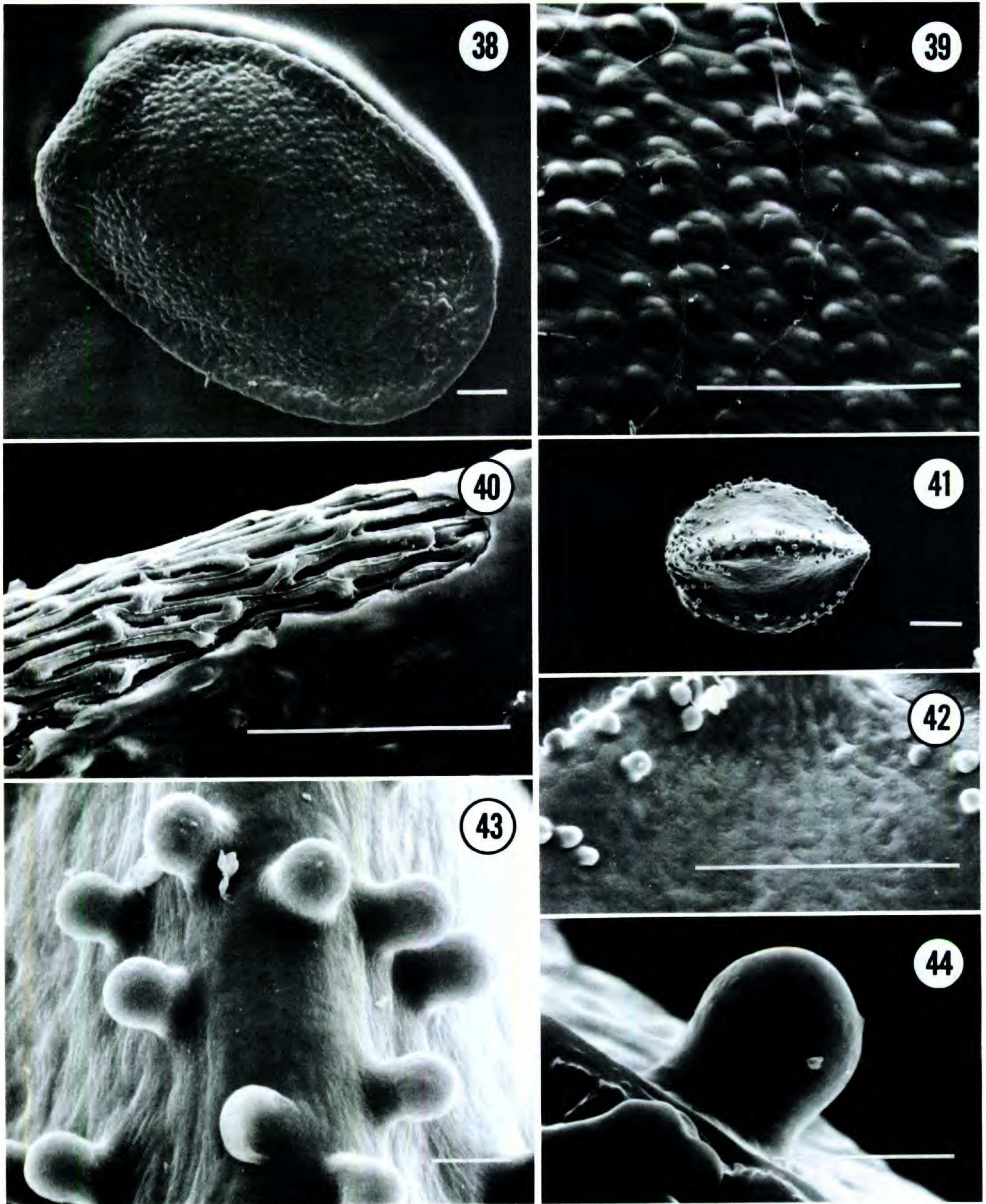
FIGURES 17–22 (bar = 100 μ m). Seeds of perennial *Campanula*.—Figures 17, 18. *Campanula uniflora*.—17. Seed (S02).—18. Seed coat (S04).—Figures 19, 20. *C. rotundifolia* s.l.—19. Seed (S89).—20. Seed coat (S89).—Figures 21, 22. *C. lasiocarpa*.—21. Seed (S25).—22. Seed coat (S25).



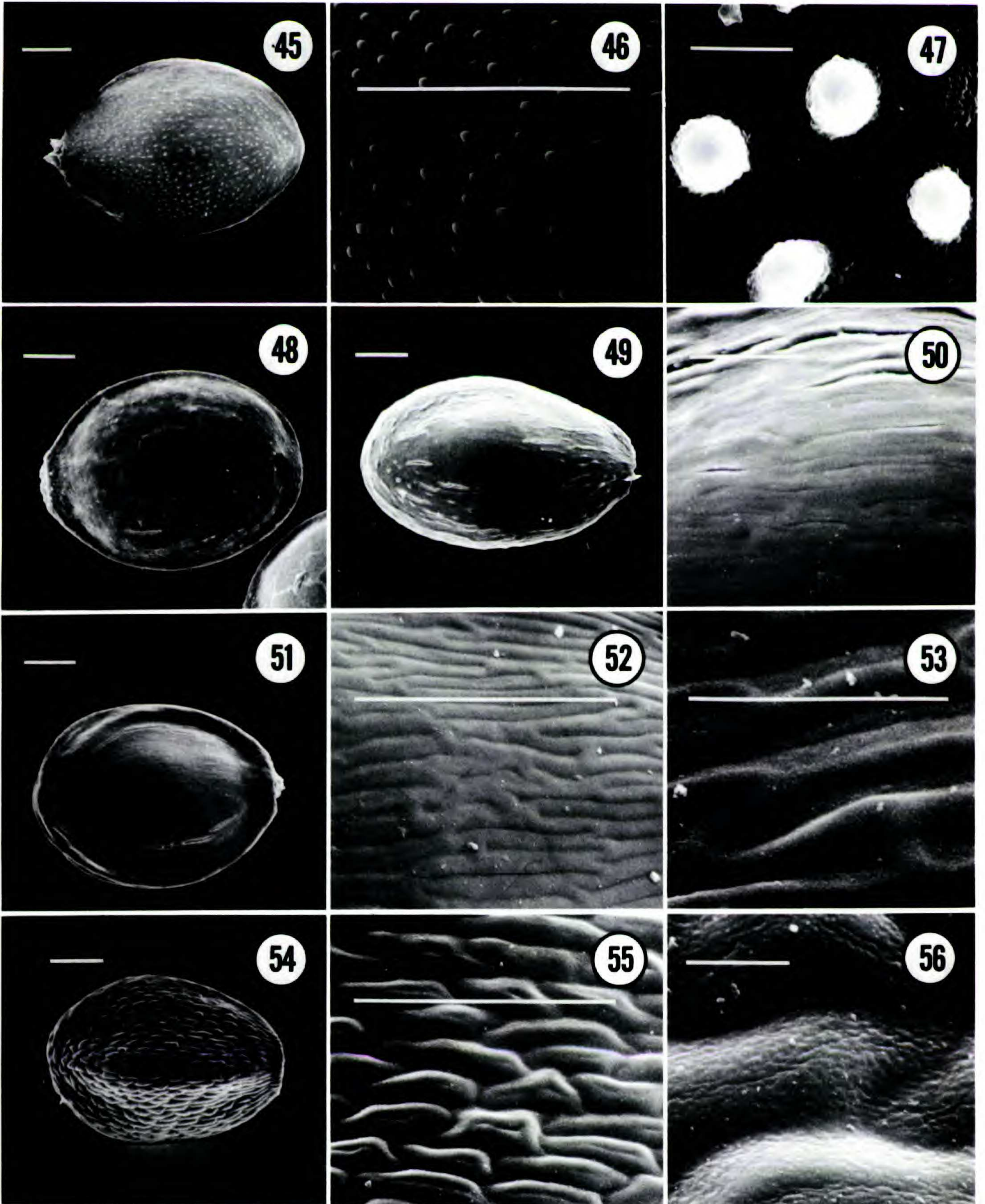
FIGURES 23–29 (bar = 100 μm). Seeds of *Campanula* and *Asyneuma*.—Figures 23, 24. *Campanula prenanthoides* (*Asyneuma prenanthoides*).—23. Seed (S08).—24. Seed coat (S08).—Figures 25–27. *C. scouleri*.—25. Seed (S05).—26. Seed coat with tangential walls collapsed (S05).—27. Seed coat with tangential walls uncollapsed (S05).—Figures 28, 29. *Asyneuma canescens*.—28. Seed (S72).—29. Seed coat (S72).



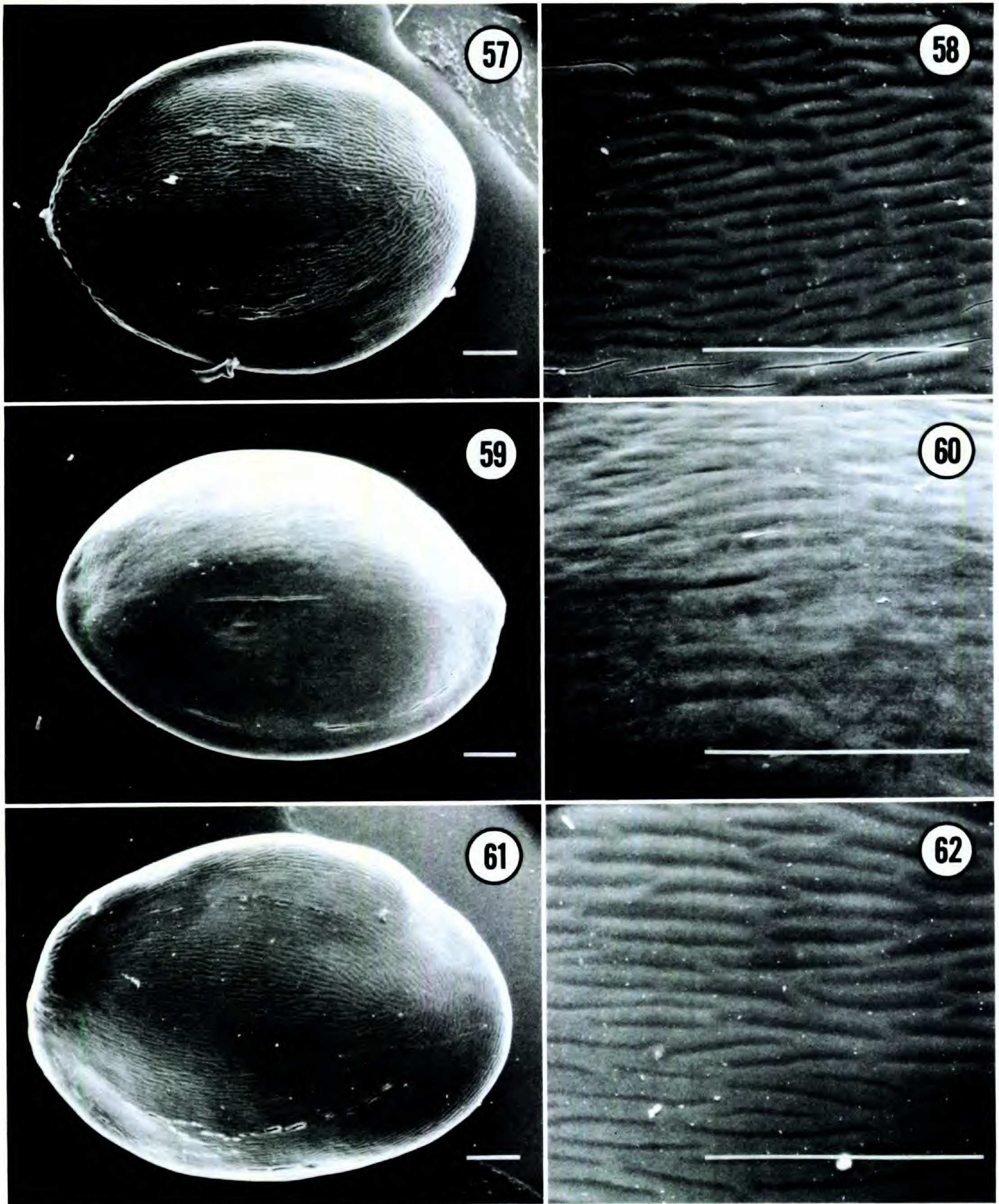
FIGURES 30–37 (bar = 100 μm). Seeds of *Campanula*.—Figures 30, 31. *Campanula aparinoides*.—30. Seed (S62).—31. Seed coat (S60).—Figures 32, 33. *C. californica*.—32. Seed (S17).—33. Seed coat (S17).—Figures 34, 35. *C. divaricata*.—34. Seed (S19).—35. Seed coat (S18).—Figures 36, 37. *C. floridana*.—36. Seed (S21).—37. Seed coat (S21).



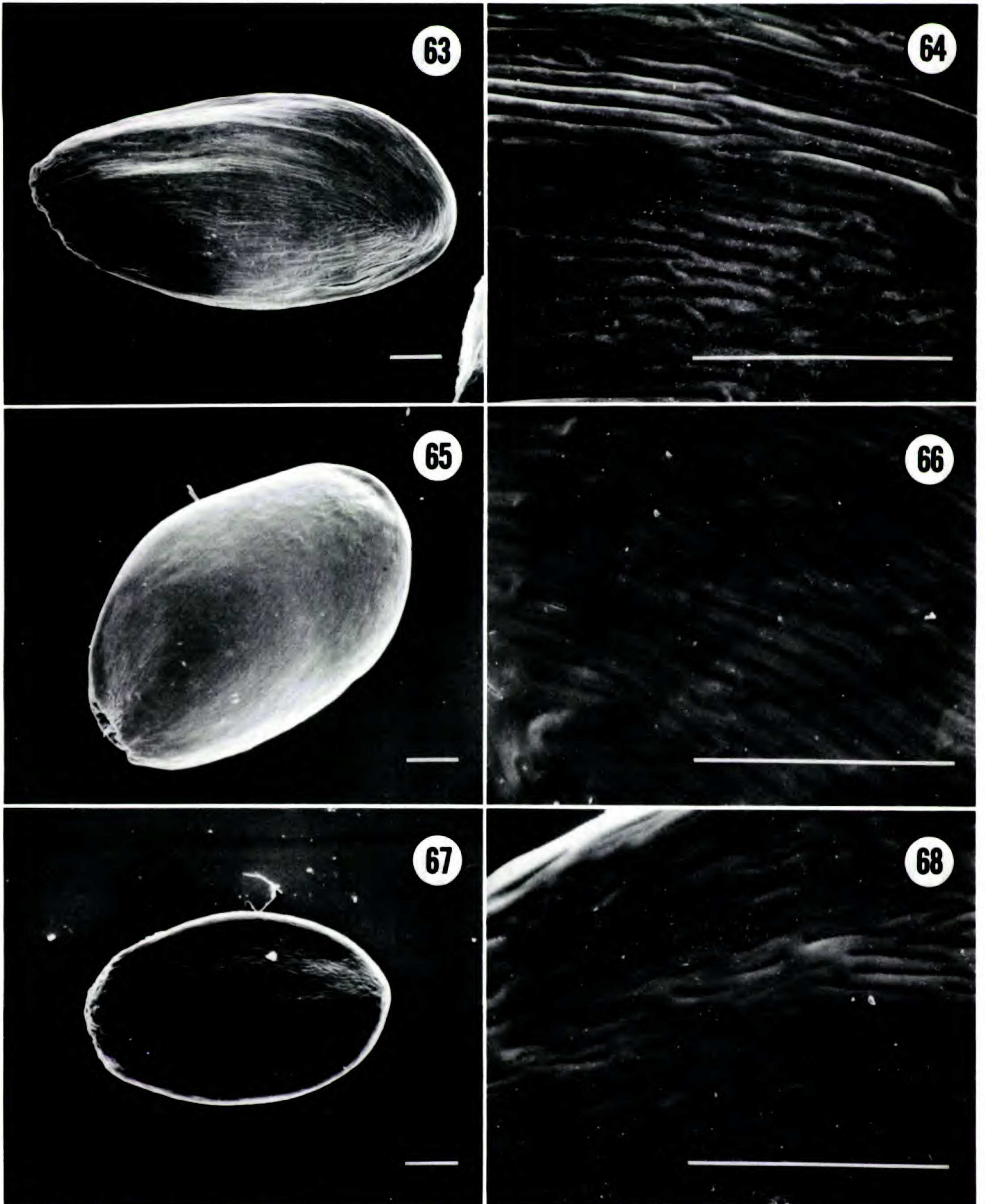
FIGURES 38–44. Seeds of *Campanula*.—Figures 38–40 (bar = 100 μm). *C. americana*.—38. Seed (S14).—39. Seed coat (S14).—40. Seed coat peeled away showing framework of cells (S13).—Figures 41–44. *C. robinisiae*.—41. Seed (S90) (bar = 100 μm).—42. Seed coat (S90) (bar = 100 μm).—43. Seed coat (S90) (bar = 10 μm).—44. Seed coat showing 1 papilla (S90) (bar = 10 μm).



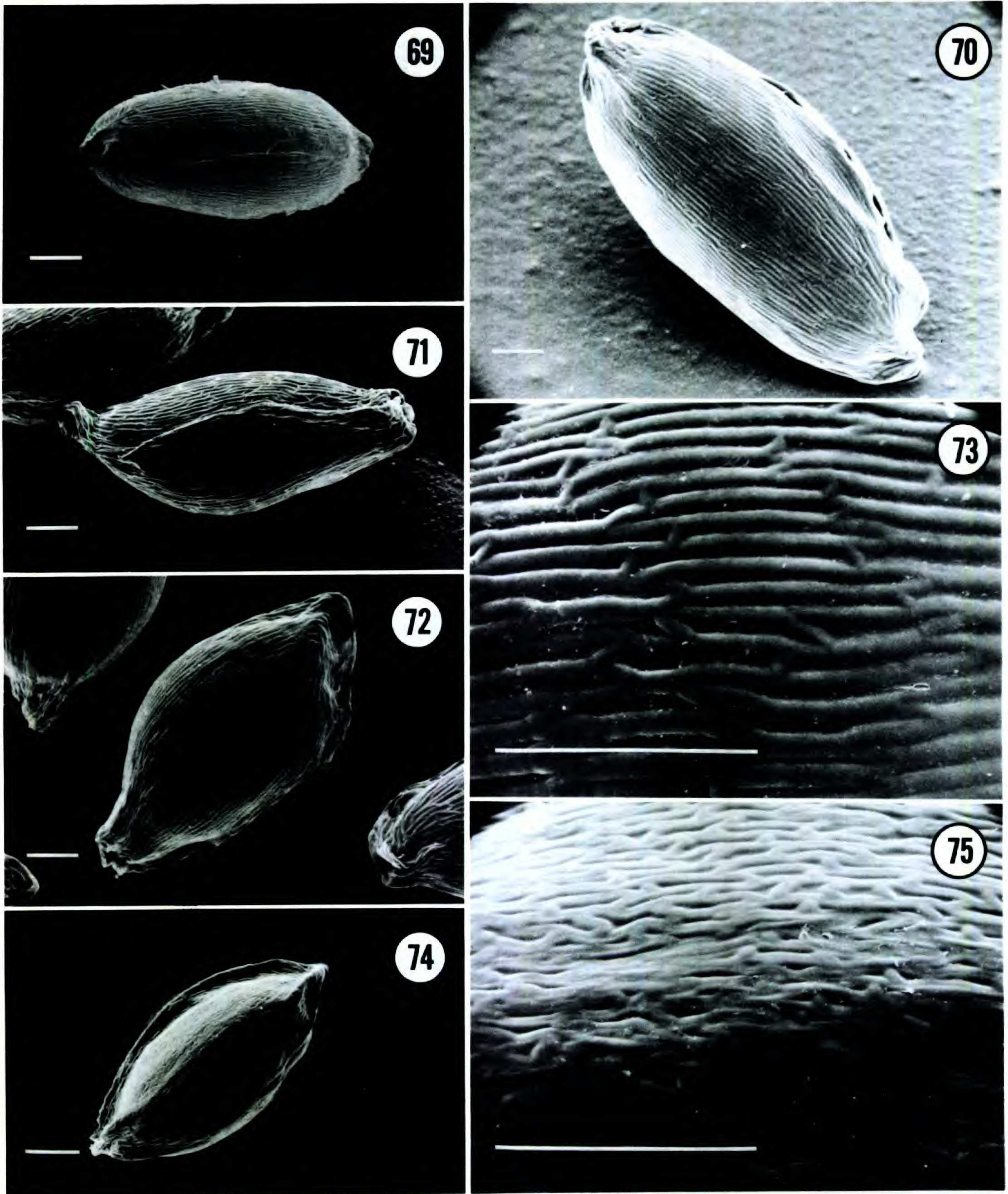
FIGURES 45–56. Seeds of *Triodanis*.—Figures 45–48. *Triodanis perfoliata*.—45. Seed of papillate type (S44) (bar = 100 μm).—46. Seed coat of papillate type (S44) (bar = 100 μm).—47. Seed coat of papillate type (S44) (bar = 10 μm).—48. Seed of smooth type (S43) (bar = 100 μm).—Figures 49, 50 (bar = 100 μm). *T. holzingeri*.—49. Seed (S36).—50. Seed coat (S36).—Figures 51–53. *T. biflora*.—51. Seed (S46) (bar = 100 μm).—52. Seed coat (S46) (bar = 100 μm).—53. Seed coat (S47) (bar = 10 μm).—Figures 54–56. *T. texana*.—54. Seed (S51) (bar = 100 μm).—55. Seed coat (S51) (bar = 100 μm).—56. Seed coat (S48) (bar = 10 μm).



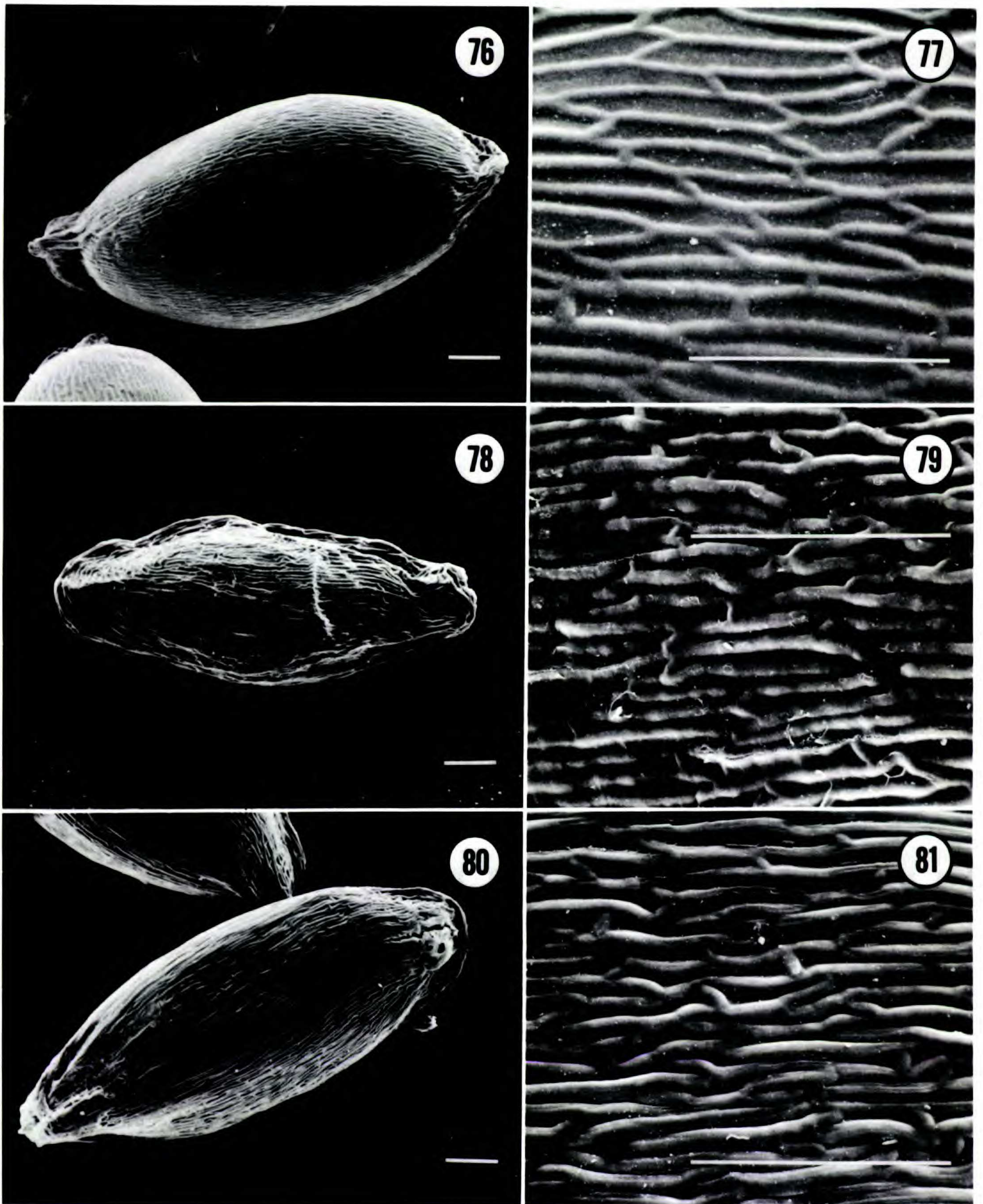
FIGURES 57-62 (bar = 100 μ m). Seeds of *Triodanis*.—Figures 57, 58. *T. coloradoensis*.—57. Seed (S34).—58. Seed coat (S34).—Figures 59, 60. *T. falcata* (*Legousia falcata* (Ten.) Fritsch).—59. Seed (S68).—60. Seed coat (S68).—Figures 61, 62. *T. lamprosperma*.—61. Seed (S39).—62. Seed coat (S39).



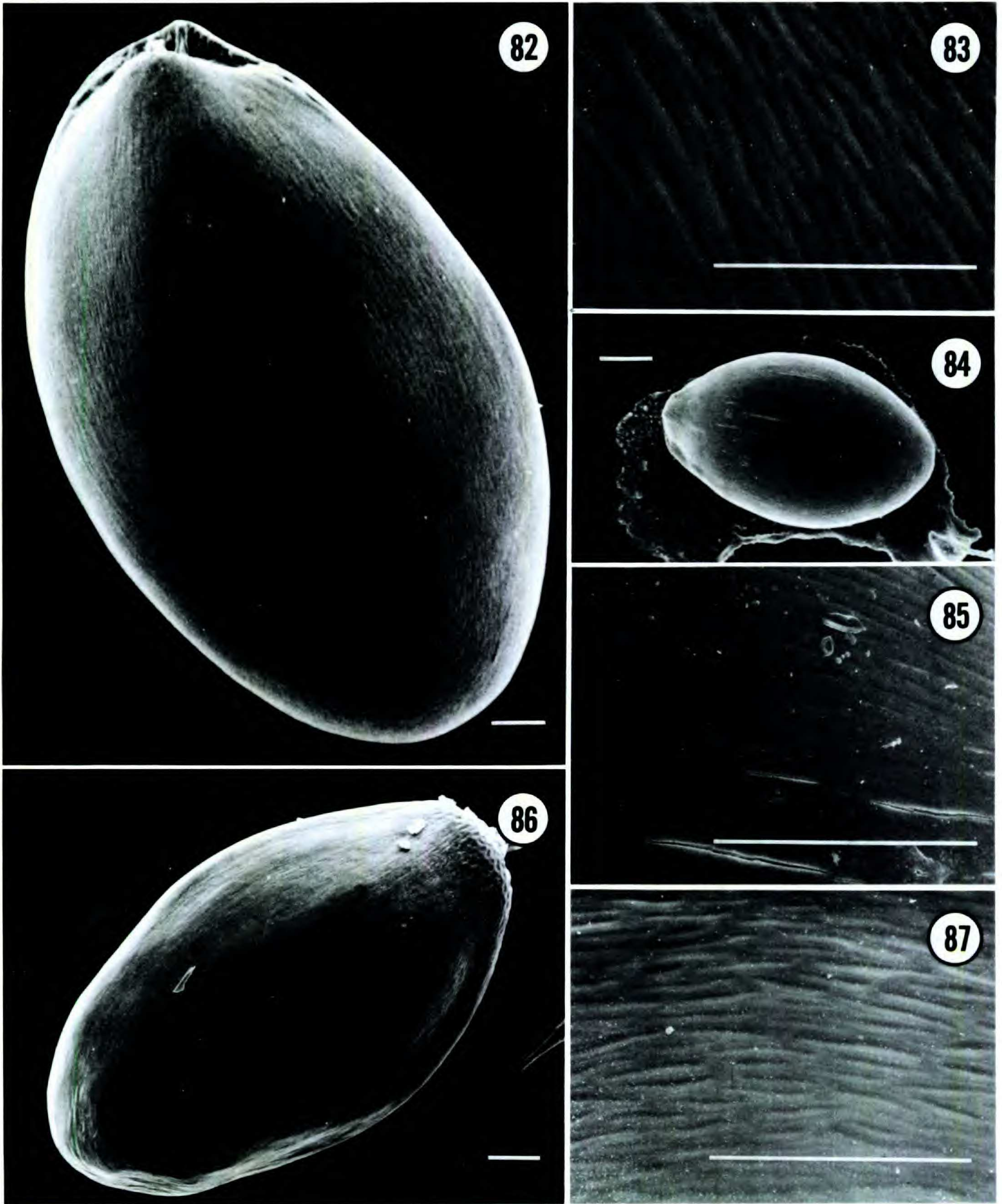
FIGURES 63–68 (bar = 100 μ m). Seeds of *Triodanis* and *Campanula*.—Figures 63–66. *T. leptocarpa*.—63. Seed (S42A, chasmogamous).—64. Seed coat (S42A).—65. Seed (S42B, cleistogamous).—66. Seed coat (S42B).—Figures 67, 68. *Campanula reverchonii*.—67. Seed (S12).—68. Seed coat (S12).



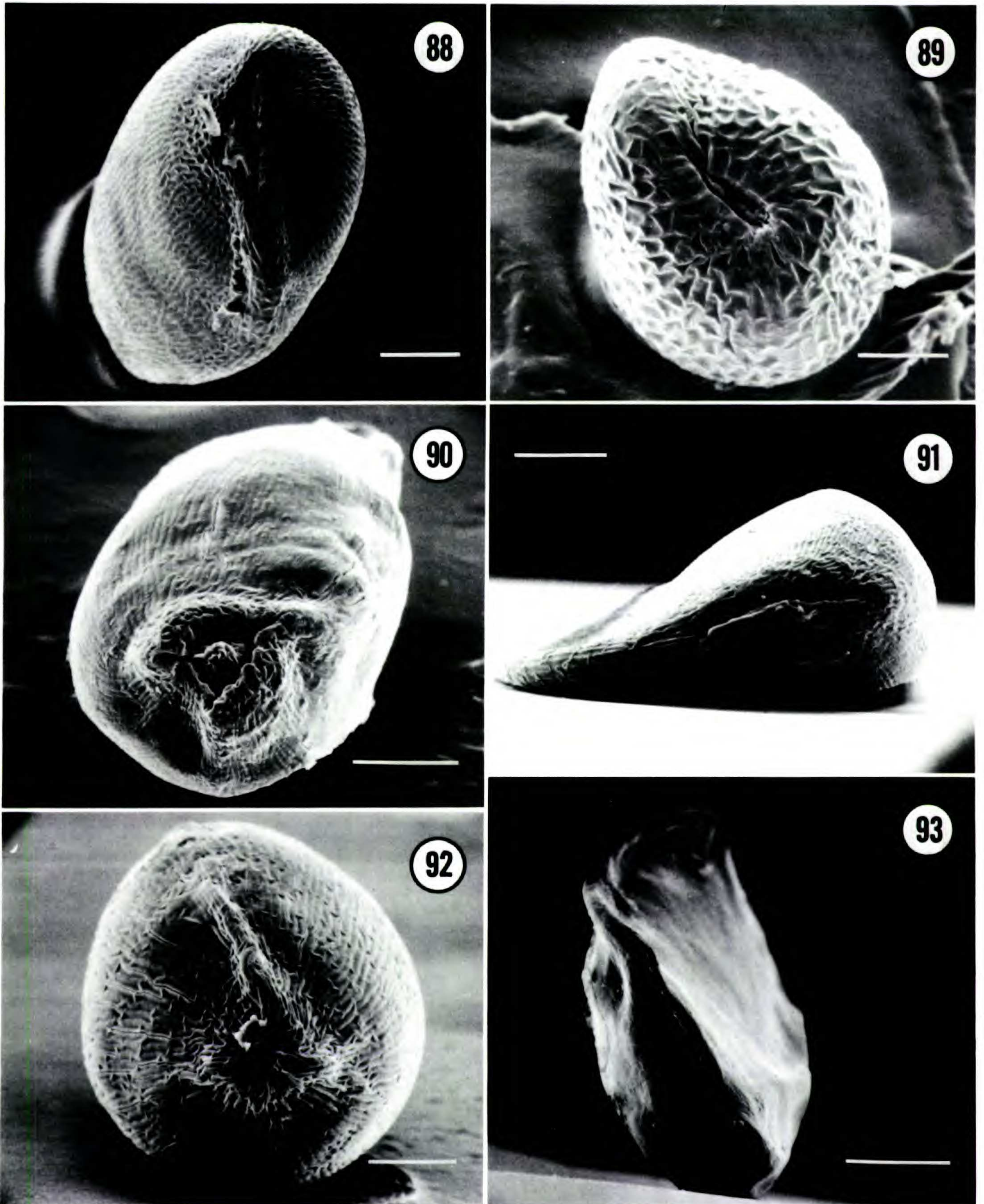
FIGURES 69-75 (bar = 100 μ m). Seeds of *Githopsis*.—Figures 69-73. *Githopsis diffusa*.—69. Subsp. *diffusa*, seed (S78).—70. Subsp. *robusta*, seed (S77).—71. Subsp. *filicaulis*, seed (S82).—72, 73. Subsp. *candida*.—72. Seed (S79).—73. Seed coat (S79).—Figures 74, 75. *G. tenella* Morin.—74. Seed (S74).—75. Seed coat (S74).



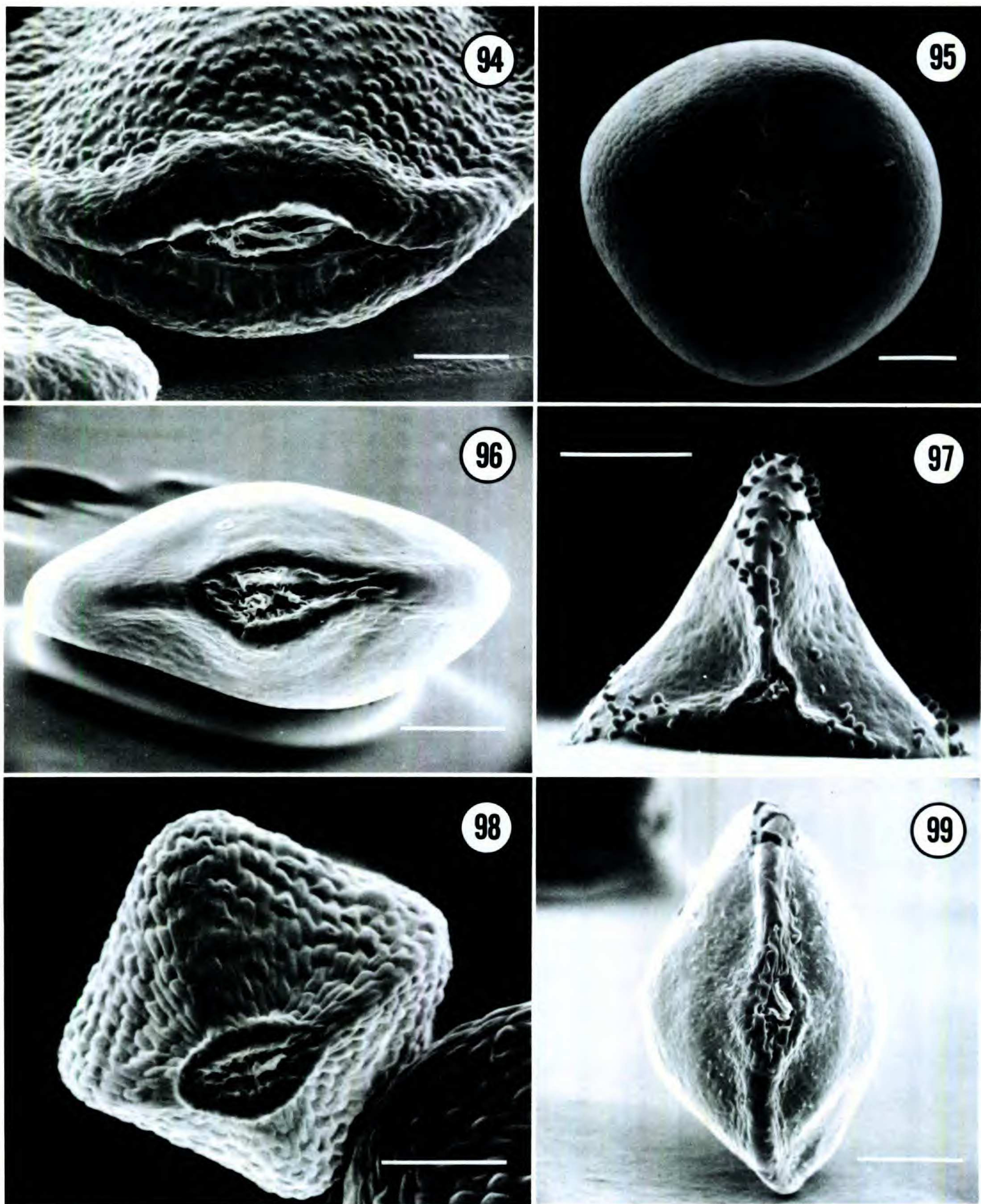
FIGURES 76–81 (bar = 100 μm). Seeds of *Githopsis*.—Figures 76, 77. *G. pulchella* subsp. *pulchella*.—76. Seed (S80).—77. Seed coat (S80).—Figures 78, 79. *G. pulchella* subsp. *serpentinicola*.—78. Seed (S81).—79. Seed coat (S81).—Figures 80, 81. *G. specularioides*.—80. Seed (S79).—81. Seed coat (S79).



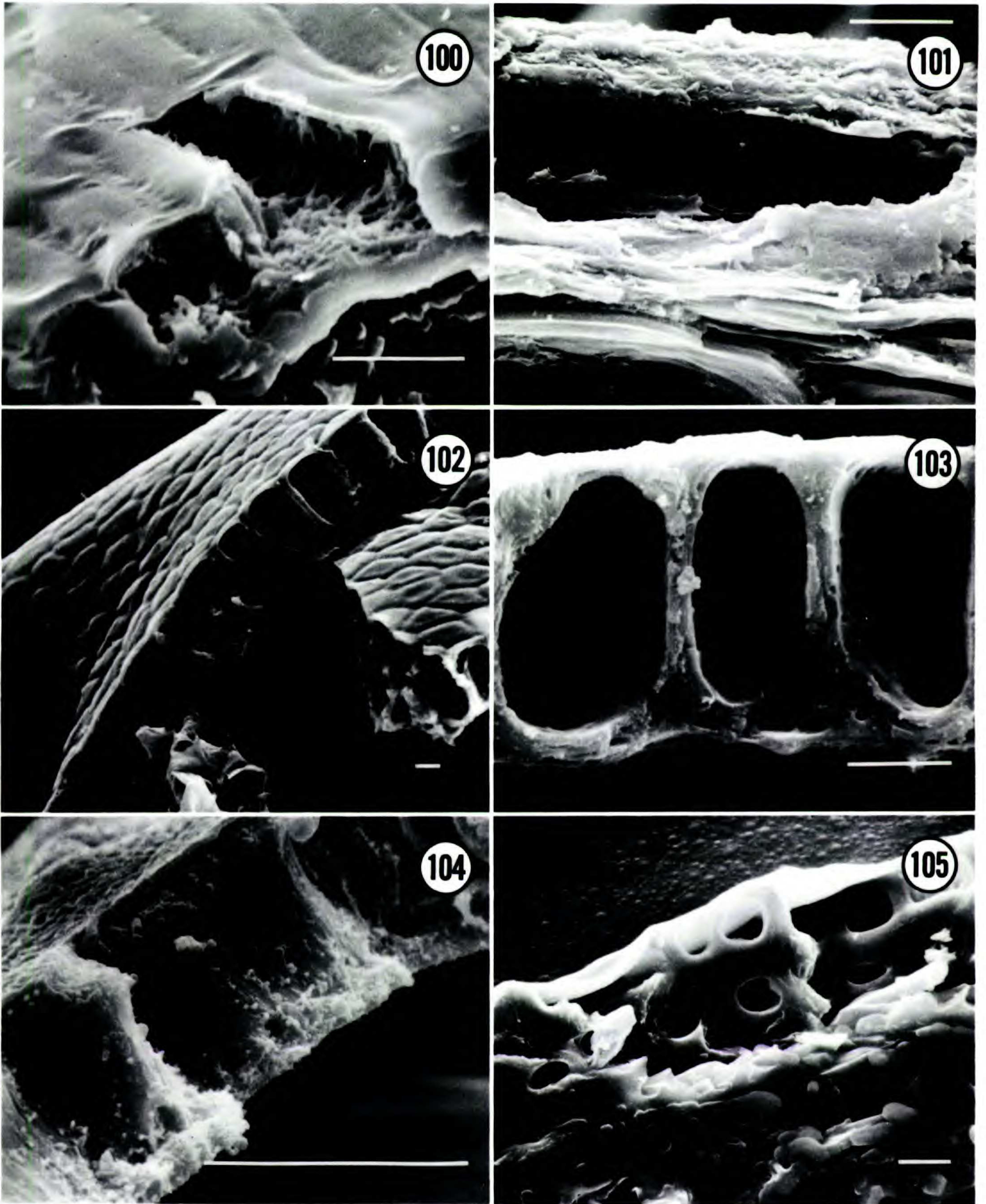
FIGURES 82-87 (bar = 100 μ m). Seeds of *Legousia* and *Heterocodon*.—Figures 82, 83. *Legousia hybrida*.—82. Seed (S67).—83. Seed coat (S67).—Figures 84, 85. *Heterocodon rariflorum*.—84. Seed (S53).—85. Seed coat (S53).—Figures 86, 87. *Legousia pentagonia*.—86. Seed (S70).—87. Seed coat (S70).



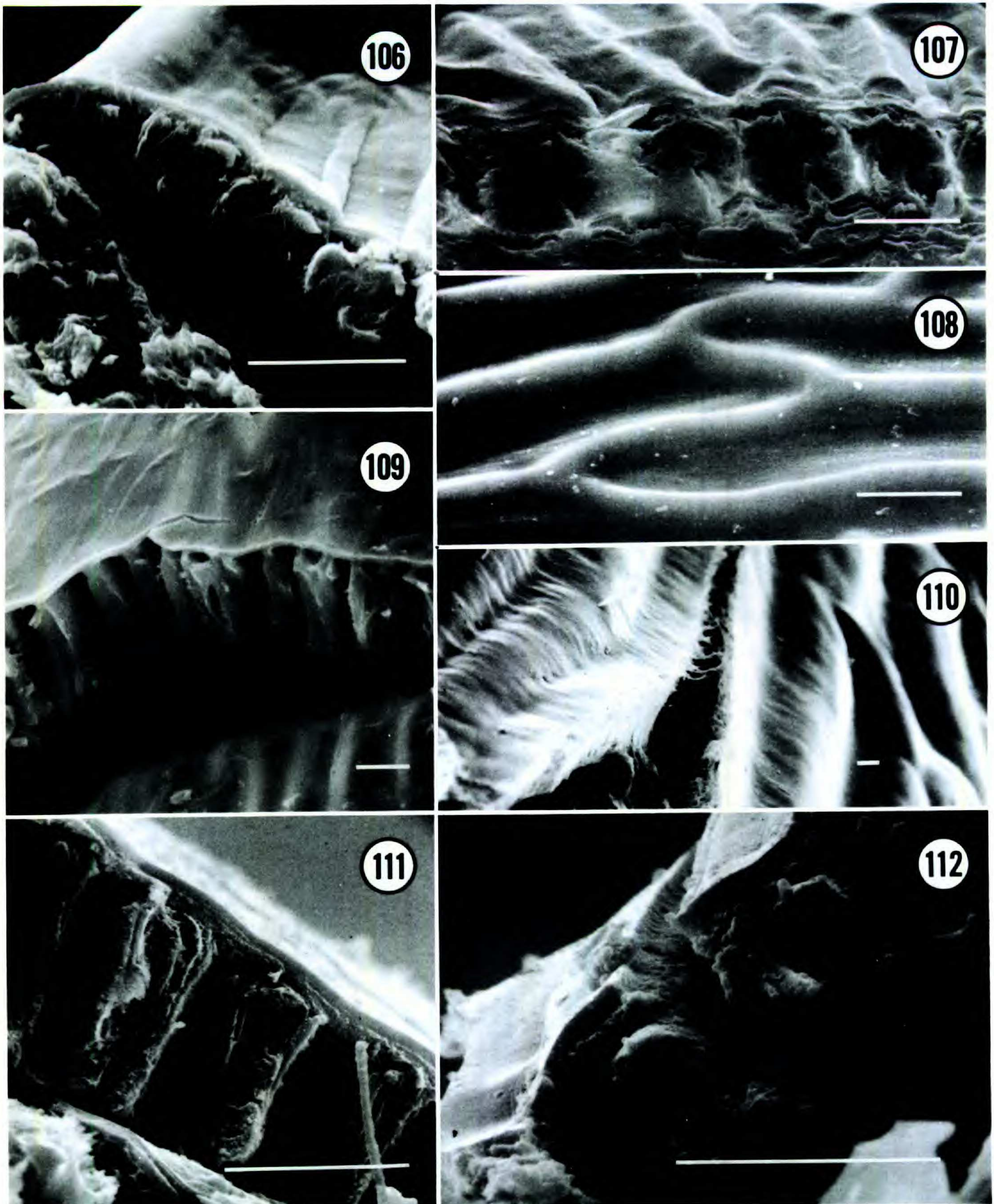
FIGURES 88–93. Face views of seeds (bar = 100 μ m).—88. *Campanula rotundifolia* (S88).—89. *C. floridana* (S21).—90. *C. lasiocarpa* (S24).—91. *C. prenanthoides* (S08).—92. *Githopsis specularioides* (S76).—93. *Campanula exigua* (S64).



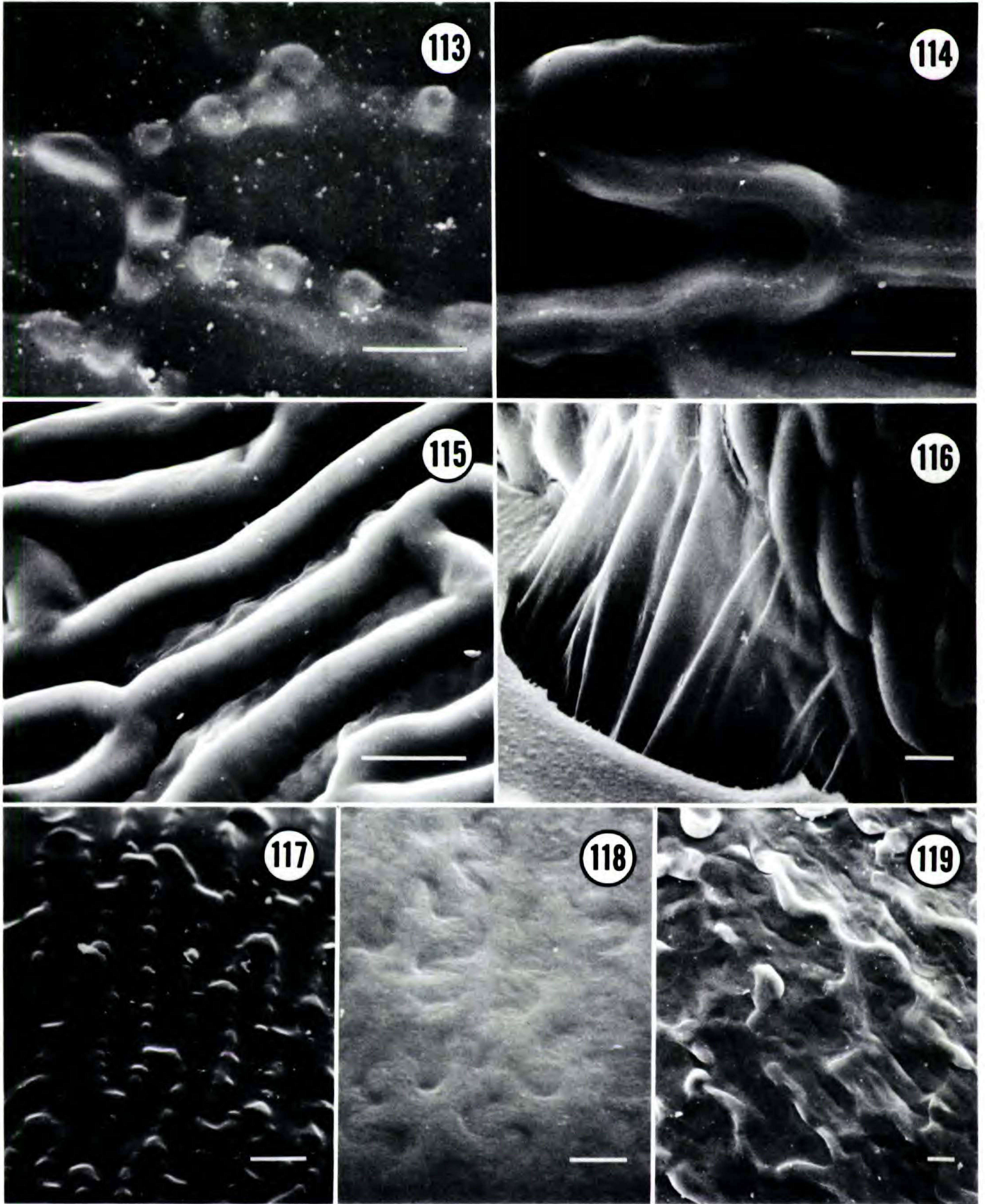
FIGURES 94-99. Face views of seeds (bar = 100 μ m).—94. *Campanula americana* (S14).—95. *C. aparinoides* (S60).—96. *C. reverchoni* (S10).—97. *C. robinsiae* (S90).—98. *Triodanis texana* (S51).—99. *T. holzingeri* (S37).



FIGURES 100–105. Seed coats in section (bar = 10 μm).—100. *Campanula uniflora* (S04).—101. *C. scabrella* (S65).—102. *C. aparinoides* (S61).—103. *C. aparinoides*, showing pits in cell walls (S63).—104. *Triodanis perfoliata* (S45).—105. *Campanula floridana*, showing wall pits (openings) (S21).



FIGURES 106–112 (bar = 10 μ m). Seed coats in section.—106. *Campanula griffinii*, seed coat in section (S85).—107. *C. rotundifolia*, seed coat in section (S88).—108. *C. rotundifolia*, seed-coat surface (S88).—109. *C. californica*, seed coat in section (S17).—110. *Githopsis diffusa* subsp. *robusta*, seed-coat surface and section (S77).—111. *Legousia hybrida*, seed coat in section (S67).—112. *Triodanis biflora*, seed coat in section (S47).



FIGURES 113–119. Seed-coat surfaces (bar = 10 μm).—113. *Campanula divaricata* (S18).—114. *C. rotundifolia* (S89).—115. *Githopsis pulchella* (S81).—116. *Triodanis texana*, cuticle (S50).—117. *Campanula parryi* (S26).—118. *C. robinsiae* (S90).—119. *Triodanis perfoliata* (S43).

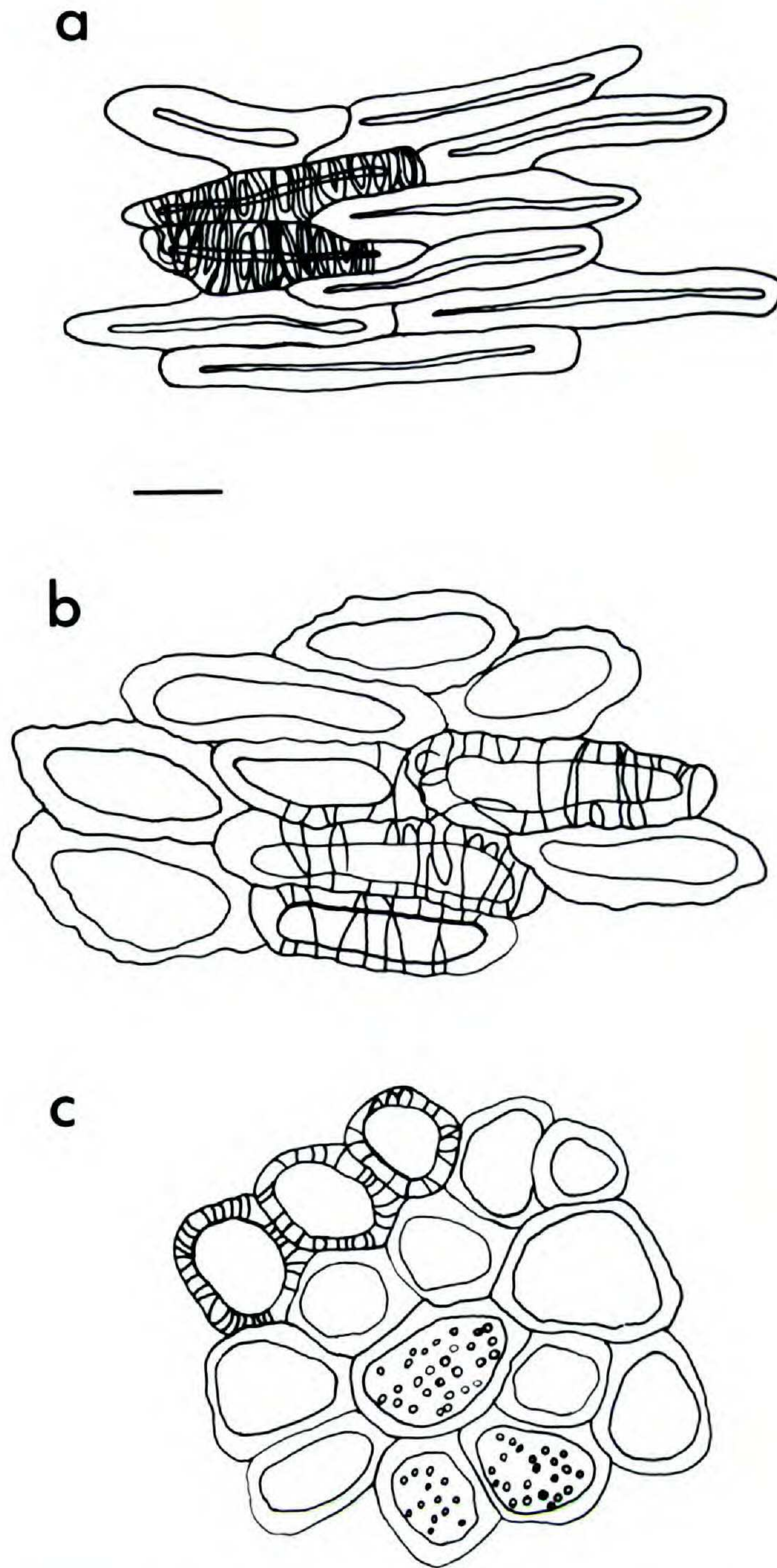


FIGURE 120. Camera lucida drawings of seed-coat peels (bar = 10 μm). Long axis of cells corresponds to long axis of the seed. Dark lines represent thickenings of radial walls; dots represent apparent pits on tangential walls.—a. *Campanula griffinii* (S85) (Type 1 pattern).—b. *C. divaricata* (S20) (Type 2 pattern).—c. *C. aparinoides* (S60) (Type 3 pattern).

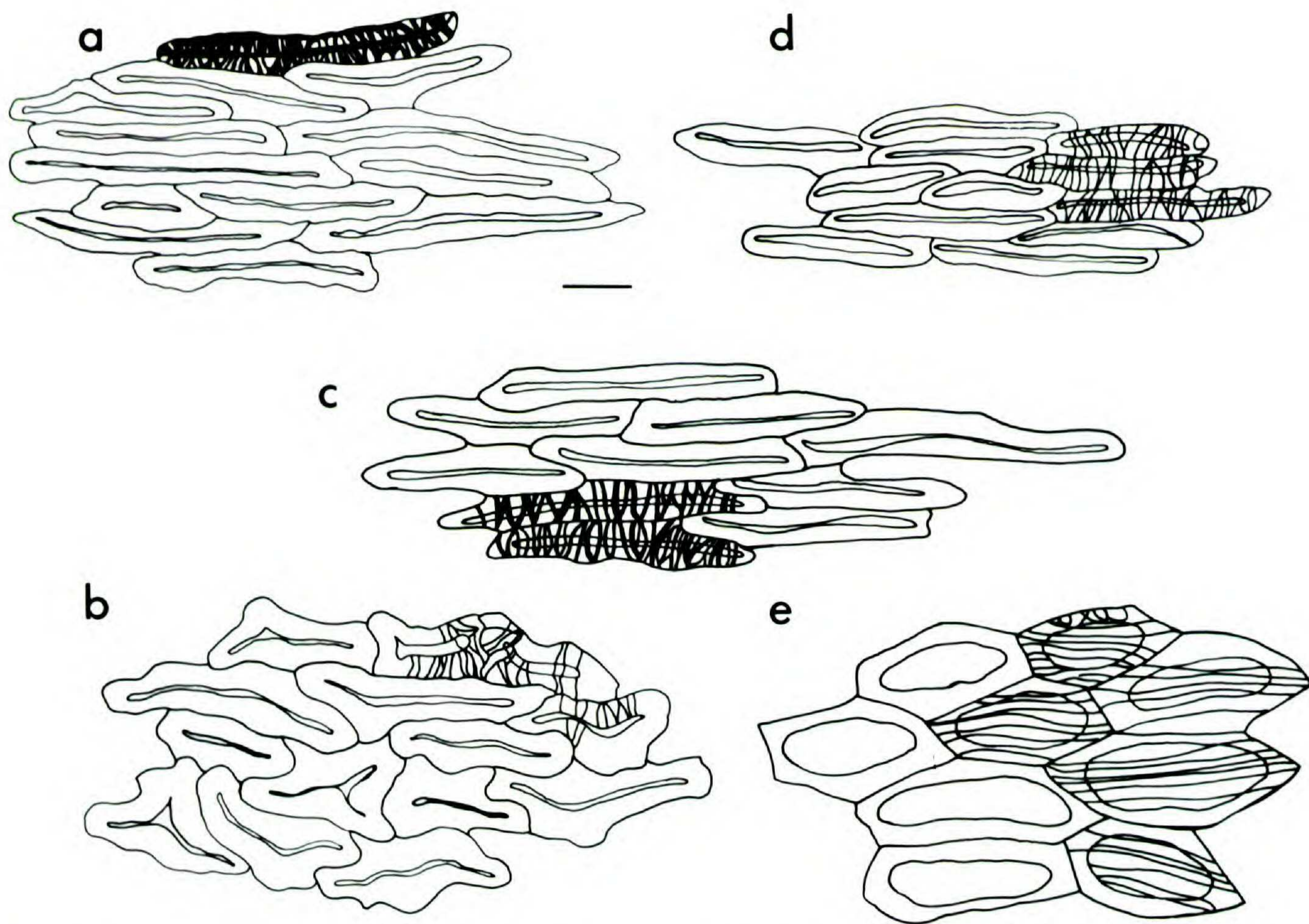


FIGURE 121. Camera lucida drawings of seed-coat peels (bar = 10 μ m). Long axis of cells corresponds to long axis of the seed. Dark lines represent thickenings of radial walls.—a. *Campanula americana* (S15).—b. *Triodanis texana* (S49B).—c. *C. piperi* (S83).—d. *C. parryi* (S27).—e. *C. floridana* (S21).

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